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THE CROONIAN LECTURES

ON

CEREBRAL LOCALISATION.

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CEREBRAL LOCALISATION.

DELIVERED BEFORE THE ROYAL COLLEGE OF PHYSICIANS,
JUNE, 1890.

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ON

CEREBRAL LOCALISATION.

LECTURE I.

INTRODUCTORY.

MR. PRESIDENT AND GENTLEMEN,—While highly appreciating the distinguished honour of being appointed Croonian Lecturer of the College of Physicians, I must confess to having undertaken the onerous duties of the office with considerable hesitation and trepidation, for, though the subject which I have chosen is one to which I have devoted a good deal of attention, and which, in one of its aspects, namely, The Localisation of Cerebral Disease, I have already had the honour of discussing before you as Gulstonian Lecturer, yet, considering the enormous amount of work that has been done in this department in recent years, and the numerous problems which still remain unsolved, I have felt that, with my other duties, time and strength would scarcely permit me to do justice to my subject. I could not feel satisfied with merely repeating the views which I have elsewhere, and at various times, expressed on this subject, and which, to many of you at least, are sufficiently well known; therefore, it seemed necessary that I should, for the purpose of these lectures, undertake new investigations, in order to throw light, if possible, upon some of the points which are still in dispute. But to compress into practically a few months of otherwise fully occupied time what might well be the undivided labour of a long period has proved a difficult task, and I have fallen far short of what I had hoped to accomplish, though I trust that some of the results at which I have been able to arrive may contribute towards a solution of some of the vexed questions. I purpose in these lectures to sketch the evolution of the doctrine of cerebral localisation, to indicate the principal data on which it is based, and to discuss, in the light of the most recent investigations, the evidence for and against the existence of specific centres, and their exact position in the cerebral cortex.

Before considering the facts bearing directly upon the specific localisation of function in the cerebral cortex, I think it advisable —nay, even necessary—to consider the effects of ablation of the cerebral hemispheres in different classes of animals. A due consideration of these phenomena affords, I think, a satisfactory explanation of the chief objections which have been urged against localisation in general, and, at the same time, also renders unnecessary certain hypotheses as to the functional substitution of one part of the cortex by another, which have been—and, in my opinion, rightly—regarded by the opponents of localisation as altogether subversive of its fundamental principles.

Recent researches on the effects of the removal of the cerebral hemispheres, by improved methods, have necessitated some important modifications of the doctrines which, up to quite a recent date, have been generally entertained on the subject.

Let us begin with fishes. When in osseous fishes the ganglia (which correspond morphologically to the cerebral hemispheres of the vertebrates) are entirely removed, there is little, if anything, to distinguish them from perfectly normal animals. They maintain their natural attitude, and use their tails and fins in swimming with the same vigour and precision as before. It has generally been said that brainless fishes possess no spontaneity, but seem as if impelled by some irresistible impulse (occasioned by the impressions communicated to the surface of their bodies by the water in which they are sustained) to swim until they are exhausted by pure neuro-muscular fatigue. In their course, however, as was shown by Vulpian, they do not blindly rush against obstacles, but turn to the right or left, according to circumstances, as if still possessed of some sense of vision. Vulpian says[1] "In fact, when the cerebral hemispheres have been removed from a fish which does not readily succumb to this kind of operation (a roach, for example), not only may it be urged to move by bringing an object before its eyes, but I have proved that it avoids obstacles; for, by placing a stick to the right or left, a few centimètres from its eye, I have frequently caused the fish to turn in the opposite direction."

Steiner[2] does not admit the absence of spontaneity in fishes so operated upon, for he has seen that they occasionally remain at

[1] *Système Nerveux*, p. 669.

[2] *Die Functionen des Centralnervensystems;* Zweite Abtheilung: *Die Fische*, 1888.

the bottom, at other times balance themselves at various heights in the water, and now and then swim about freely, without any obvious alterations in the conditions by which they are surrounded. He has also shown, and in this he has been confirmed by Vulpian,[3] that they not only see, but are able to find, their food. If worms be thrown into the water in which they are swimming, they immediately pounce upon them. If a piece of string similar in size to a worm be thrown in, they are able to detect the difference, and either disregard it entirely, or drop it after having seized it. Not only do they seize their food, but they discriminate between different kinds, selecting some, and rejecting others. They even to some extent distinguish colours, for when one red and a few white wafers are thrown into the water, the fish almost invariably selects the red in preference to the white.

From these facts it would appear that the fish without cerebral hemispheres can see, distinguish colours to some extent, catch its prey, discriminate between different kinds of food, direct its movements with precision, and, in fact, behave to all appearance like a normal animal. The only difference observed by Steiner was that brainless fishes appeared more impulsive and less cautious than those which had not been operated upon.

What has been said above applies, however, only to Teleosteous fishes. Quite different results appear to follow removal of the cerebral hemispheres in Elasmobranchs. Thus the dog-fish, according to Steiner,[4] after this operation is entirely deprived of spontaneity, and is quite unable to find the food (sardines) by which it is surrounded. The difference between the two orders of fishes is, however, more apparent than real, for the dog-fish is guided mainly by its sense of smell, while the activity of the osseous fish is conditioned more especially by vision; hence, in the dog-fish, removal of the cerebral hemispheres, which are almost exclusively related to the sense of smell (Fig. 1.—A), abolishes all the reactions conditioned by this sense; while in the osseous fish, the primary visual centres (optic lobes), being intact, the ordinary modes of activity, which are conditioned mainly by the eyes, continue to all appearance unmodified.

Frogs.—According to the researches, more particularly of Goltz[5] and Steiner,[6] frogs deprived of their cerebral hemispheres behave,

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[3] *Comptes Rendus.* Tome 102 and 103, 1886.
[4] *Op. cit.*
[5] *Functionen der Nervencentren des Frosches*, 1869.
[6] *Physiologie des Froschhirns*, 1885.

cæteris paribus, essentially like fishes similarly treated; they maintain their normal attitude, and resist all attempts to overthrow their equilibrium. If laid on their backs they will turn over and attempt to regain their ordinary position. If the basis of support on which they rest is tilted in any direction, they will clamber up, forwards, or backwards until they gain a position of stability. Their powers of locomotion are retained, and their limbs are co-ordinated with precision. If a foot be pinched, or any irritation applied to the posterior part of the body, they will hop away; thrown into the water they will swim, and continue swimming until they have reached the side of the vessel, up which, if possible, they will clamber and rest in peace. It would, in fact, be difficult, so far as their movements and response to

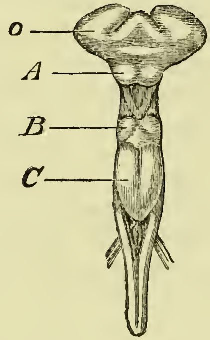

Fig. 1.—Brain of dog-fish (after Steiner). A, cerebral hemisphere; B, optic lobe; C, cerebellum; O, olfactory lobe.

peripheral stimuli are concerned, to distinguish between a normal and a brainless frog. If the back be gently stroked the frog will answer uniformly with a croak, as if of pleasure or enjoyment. If the animal be put in a vessel containing water, the temperature of which is gradually raised, it will jump out as soon as the bath becomes uncomfortably hot. If placed at the bottom of a pail of water, it will ascend to the surface to breathe. If the vessel be inverted over a pneumatic trough and filled with water, sustained by barometric pressure, the frog will ascend to the top as before, but not finding there the oxygen necessary to satisfy its respiratory craving, it will work its way downwards, and ultimately succeed in making its escape out of the vessel on to the free surface of the trough. Like the fish, the brainless frog undoubtedly possesses some form of vision; it does not, when urged to move, rush blindly against an obstacle, but will leap over it, or turn to the right or left, or otherwise avoid it. In all these respects a brainless frog behaves like a normal one, but one noteworthy difference has been signalised by most observers—namely, that the brainless frog, unless disturbed by some form of peripheral stimulus, will remain for ever quiet on the same spot, until, in fact, it becomes dried up and converted into a mummy. All spontaneity—that is, varied activity under apparently the same external conditions—appears to be annihilated; its past experience has been blotted out, and it views with indifference signs and threats which would formerly have made it flee. It is also generally stated that the brainless frog has lost its instincts of self-preservation, and either feels no hunger or possesses no power to satisfy its physical necessities, so that it dies in the midst of plenty. The more recent experiments, however, of Schrader[7] would seem to show that removal of the hemispheres deprives the frog neither of spontaneity, nor of special instincts, nor of the ability to feed itself; for he has observed brainless frogs which have been kept alive for long periods, apparently "spontaneously" jump from the pier of a galvanometer, absolutely free from all tendency to vibration, alternate between land and water in the aquarium, crawl under stones, or bury themselves in the earth at the beginning of winter, and, when cautiously submerged under water, begin to swim exactly like normal frogs under the same conditions. These frogs also, after the period of hybernation, or in the summer, when their wounds were entirely healed, diligently caught the flies that were buzzing about in the vessels in which they were kept. It would appear, therefore, if these observations are correct, that the principal points of distinction between the brainless and the normal frog—namely, the absence of spontaneity and the power to feed itself, which are said to especially characterise the former—are no longer capable of being upheld, and that the brainless frog behaves precisely like the brainless fish above described.

Birds.—Let us now proceed to consider the effects of the removal of the cerebral hemispheres in birds, the next higher class of vertebrates, and more especially in pigeons. These have been rendered familiar to all by the classical researches of Flourens;[8] but though the picture he has drawn has been accepted as in the main correct, there have been, and there still are, some differences of opinion as to the facts, and more particularly as to their mode

[7] Physiologie des Froschgehirns, *Pflüger's Archiv für Physiologie*, 1887, Band 41

[8] *Système Nerveux*, 1842.

of interpretation. There is, however, no doubt that after this operation pigeons show no disturbance of station or locomotion. They maintain their normal attitude, and resist all attempts to overthrow their balance. Left to themselves they appear, at first at least, to be plunged in profound sleep. From this condition they are easily aroused by a gentle push or pinch. When so urged they march forwards, and should they happen to step over the edge of the table, on which they are placed, they will flap their wings and regain their base of support. Thrown into the air they fly with all due precision and co-ordination. After each manifestation of activity so induced they subside into their original state of repose. Occasionally, and apparently without any external stimulus, they may look up and yawn, shake themselves, dress their feathers with their beaks, move a few steps forwards or backwards, especially after defæcation, and then settle down quietly, standing sometimes on one leg, sometimes on the other. They are altogether unable to feed themselves; but, if fed artificially, deglutition, digestion, and nutrition go on in a normal manner, and the animals may be kept alive for an indefinite period. Flourens was of opinion that the removal of the cerebral hemispheres annihilated all the senses, and rendered the animals blind, deaf, and devoid of smell, taste, and tactile sensibility. These conclusions were, however, disputed by Magendie, Bouillaud, Cuvier, and, in particular, by Longet[9] and Vulpian.[10] Longet found that the animals appeared to see, inasmuch as they would follow the movements of a flame held in front of their eyes at a sufficient distance to prevent all sensation of heat, and also when urged to move, occasionally at least, avoided obstacles in their path. Also they started at loud sounds, such as a pistol shot, made in their immediate vicinity; and from their movements and gestures appeared to feel impressions made upon the nerves of common sensation. As regards the senses of taste and smell, he found it impossible to arrive at any definite conclusions in animals of this order, and looked upon the statements of Flourens as not supported by convincing evidence. Longet believed that the removal of the cerebral hemispheres annihilated only perception proper, as distinct from crude or brute sensation, which had its centre in the mesencephalic ganglia.

The question as to the sense of sight in brainless pigeons has been much discussed, that is, whether not mere impressionability

[9] *Anatomie et Physiologie du Système Nerveux*, 1842.
[10] *Op. cit.*

to light exists, but as to whether the animals see, in the sense of being able to guide their movements in accordance with their retinal impressions. McKendrick[11] was of opinion that removal of the one cerebral hemisphere caused blindness in the opposite eye; and Jastrowitz,[12] from his own experiments, arrived at the same conclusion (on this see further below). The experiments of Blaschko,[13] under the direction of Munk, led to no very definite conclusions on this point, though it seemed as if the removal of the one hemisphere did not cause total blindness in the opposite eye. But Munk himself[14] has made it the subject of a considerable number of experiments. He found that in a certain number of pigeons, from which he had attempted to remove the cerebral hemispheres, vision was not entirely abolished, and the animals were able to avoid obstacles placed in their path. Careful investigations, however (*post mortem*) revealed the fact that in such cases the hemispheres had not been entirely destroyed, vision continuing to some extent in the eye opposite the hemisphere, the extirpation of which had not been absolutely complete. In those cases, however, in which not a trace of either hemisphere was allowed to remain, blindness was complete and absolute. These animals, in their attitude and reaction to peripheral stimuli, etc., exhibited the symptoms already described. The brightest light, however, caused no result beyond contraction of the pupil. The animals, when urged to move, ran against every obstacle which came in their way. When thrown into the air, they flew with retracted head and half-raised trunk, outstretched legs, and dashed against obstacles, or fell bump on the ground and slid a considerable distance before coming to a standstill.

The phenomena described by Munk certainly indicate total blindness on the part of his pigeons, and he is of opinion that all those who have held that ablation of the cerebral hemispheres does not cause total blindness are in error, owing to the fact of the extirpation of the hemispheres not having been complete. Schrader, however,[15] describes the phenomena which he observed in two pigeons, from which, according to the *post-mortem* examination of von Recklinghausen, he had entirely removed every por-

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11 Observations and Experiments on the Corpora Striata and Cerebral Hemispheres of Pigeons, Royal Society, Edinburgh, 1873.

12 Ueber die Bedeutung des Grosshirns, *Archiv. für Psychiatrie*, 1876.

13 *Das Sehcentrum bei Fröschen*, Berlin, 1880.

14 "Uber die centralen Organe für das Sehen und das Hören bei den Wirbethieren; *Sitzungsberichte d. Berlin Akademie d. Wissenschaften*, July, 1883.

15 Physiologie des Vogelgehirns, *Pflüger's Archiv*, Bd. 44.

tion of the cerebral hemispheres. None of the cortex remained, but only minute remnants of the cut cerebral peduncles, which were, moreover, in a state of softening. These pigeons, within a few days after the operation, behaved in such a manner as can only be explained by their still retaining some form of vision. For they not only avoided obstacles in their path, or in their flight, but appeared able to fly from one place and alight securely on another. These flights were mostly, if not entirely, caused by conditions calculated to induce a change of position, such, for instance, as mounting them on a narrow basis of support, or putting them through balancing experiments. They never on any occasion spontaneously flew upwards from the ground.

With respect to the sense of hearing, Schrader verified in some of his animals the observations of Longet, that loud sounds, like the explosion of a percussion cap, caused a sudden start, but beyond this there were no signs of impressionability to auditory stimuli. If the results described by Schrader are correct, and of this the description given by himself and von Recklinghausen seems to leave little room for doubt, we shall then be obliged to class birds with fishes and frogs, which without doubt retain their sense of sight, and guide their movements accordingly, notwithstanding the complete removal of their cerebral hemispheres.

Mammals.—While removal of the cerebral hemispheres (including corpora striata) in the lower vertebrates is compatible with survival for a considerable length of time, the case is different with mammals. In these the operation causes fatal shock, or is followed by secondary effects which result in speedy death. For this reason it has not been found possible to determine, as in the lower vertebrates, what functions, after considerable lapse of time, might still be exhibited by the lower centres in the entire absence of the higher. The mammals on which the operation has succeeded best have been chiefly of the lower orders, such as rabbits, guinea-pigs, and rats. When the hemispheres have been removed from a rabbit or a guinea-pig, the animal, at first utterly prostrate, begins after a varying interval, say from half an hour or more, to exhibit a capacity for the performance of actions of a considerable degree of complexity. The muscular power of the limbs has, however, become enfeebled to a noteworthy extent, and, relatively, much more so in the fore than in the hind limbs. It is, nevertheless, able to maintain its equilibrium, but sits huddled up, while the legs tend to sprawl, or are planted in unnatural positions. It resists attempts to overthrow its balance, and if disturbed regains its former attitude. If the foot or tail be pinched, the animal will bound forward in its characteristic mode of progression, and again settle down when the effect of the stimulus has worn off. It may shake its ears, slightly change its position, rub its snout with its paws, or scratch its body, and again subside into a condition of perfect quiescence. The pupils contract when a light is thrown into the eye, and the eyelids wink when the conjunctiva is touched. Loud sounds will cause the ears to twitch, or provoke a sudden start. According to Longet, colocynth placed in the mouth will cause movements of the tongue and organs of mastication, in all respects resembling those of disgust, and efforts to get rid of the nauseous taste. Ammonia held before the nostrils will cause a sudden retraction of the head, or induce the animal to rub its nostrils with its paws. Not merely does it respond by movements to a pinch or prick of its foot or tail, but, if the stimulation be more severe, it will utter repeated and prolonged cries of a plaintive character. All spontaneity seems to be abolished; but it is usual for the animals, after the period of quiescence has passed, to make apparently spontaneous running movements, which, however, are found to depend upon irritation caused by the secondary changes set up in the wound.

Whether after removal of the cerebral hemispheres rabbits and other rodents can see, is a question which has been the subject of lively controversy between Christiani and Munk.[16] Christiani, after careful severance of the hemispheres and corpora striata immediately anterior to the optic thalami, states that he has seen rabbits pass and repass obstacles, such as legs of chairs and tables, and is of opinion that, though they do not see like normal rabbits, they are still able to guide their movements in accordance with retinal impressions. Munk, on the other hand, denies the accuracy of Christiani's experiments, and holds that rabbits, after removal of the cerebral hemispheres, are absolutely blind, and show no indications whatever that they are influenced by light, except as regards the contraction and dilatation of the pupils. He believes that the apparent avoidance of obstacles by Christiani's rabbits was a pure accident, as the obstacles did not happen to lie in their path.

The question is one which cannot be said to be definitely settled though the facts mentioned in respect to fishes, frogs, and birds would incline one to believe that Christiani's results and conclusions may have a solid foundation. On this point, however, and

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16 *Physiologie des Gehirnes*, 1885.

on others relating to the sensory and motor faculties of brainless mammals it is difficult to arrive at altogether satisfactory conclusions, as they, unlike the lower vertebrates, have as a rule so speedily succumbed to the operation. Hence, the lower animals' centres have no time to recover from the shock which must necessarily ensue from such a violent rupture of the solidarity previously existing between them and the highest centres. As the cause of death in mammals seems largely dependent upon secondary (inflammatory and other) consequences, and not on the mere fact of removal of the hemispheres themselves, it is much to be desired that some method may be discovered whereby the animals may be maintained alive longer than has hitherto been found possible. The nearest approach to this has been attained by Goltz,[17] who has made a series of careful observations on dogs for prolonged periods, after very extensive destruction of both cerebral hemispheres. Though the destruction has been far from complete in any case, yet the phenomena described by him teach lessons of the utmost importance in the comparative physiology of the brain. Goltz himself has utilised these experiments as the bases of his polemic against cerebral localisation, but we may, for the time, abstract from their bearing in this direction, and consider the facts themselves which he has recorded.

Goltz [18] thus describes a dog in which he had by repeated operations destroyed a large extent of both hemispheres. The amount of primary destruction, together with the secondary atrophy so induced, was so great that the whole brain weighed only 13 drachms instead of 90, which should have been the weight of a normal brain in an animal of the same size. This dog had a profoundly demented, expressionless face. Left to itself it wandered about restlessly, paying no attention to what was going on around it. All its movements were awkward and unsteady, but it exhibited no complete paralysis. It slipped, however, on a smooth surface, and its legs tended to sprawl from under it, so that it would fall upon its abdomen. From this position it would recover itself and again begin its walk. It had the utmost difficulty in feeding itself, though it could find its food when placed in the customary corner of its cage, yet it seemed unable to find it when placed in an unusual position, and even when the food was brought directly under its nose it would snap aimlessly as often outside the dish as in it. It was utterly unable to use its paws

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17 Verrichtungen des Grosshirns, *Pflüger's Archiv*, 1876-1888.

18 *Op. cit.*, p. 134.

for holding and gnawing a bone. It paid no attention to strangers, men or animals; did not wince at the brightest light suddenly thrown in its eyes, and exhibited no fear at any kind of threat. Though it appeared absolutely blind, yet numerous and varied experiments demonstrated that it was able to guide its movements by sight. It did not run against obstacles as it invariably did when its eyes were blindfolded. It was not deaf, for it could be waked out of sleep by a loud sound, but the character of the sound made no further impression upon it. It did not heed tobacco smoke or chloroform vapour, and would eat a piece of wood as readily as a bone. It did not appear to be influenced by the proximity of another dog. It exhibited no emotion of anger when another stole its food, nor did it express pleasure in the usual way by wagging its tail. Its cutaneous sensibility was everywhere diminished, but no part was absolutely without feeling. If its foot was severely pinched it would draw its leg back and bite angrily.

The symptoms exhibited by this dog and another similarly operated upon are thus summed up by Goltz: "Both animals were essentially only wandering, eating, and drinking reflex machines. Both were utterly indifferent to man and beast. Both had obtuseness of all their senses. Each had sensation in every part of its skin, and effected movements with all its muscles. Neither exhibited any expression of pleasure; on the other hand, both were easily roused to wrath. Both were profoundly demented."

The impairment of all the sensory and motor faculties in these and other dogs operated upon by Goltz—in which it is certain that not one of the specific centres was entirely destroyed—would without doubt have been more prôfound than in rabbits and guinea-pigs had it been possible to extirpate the hemispheres entirely. And when we come to consider the effects of partial cerebral lesions in man, we shall see reason for believing that if in him the whole of the hemispheres were removed, providing this were compatible with life, there would be such complete and enduring paralysis of motion, and annihilation of all the forms of sense, that scarcely a trace would remain to those responsive and adaptive reactions which survive the removal of the cerebral hemispheres in animals lower in the scale.

It thus appears that, notwithstanding the complete extirpation of the cerebral hemispheres, animals, in proportion to their lowness in the scale, besides duly maintaining and regulating all their organic functions, remain possessed of varied powers which may be classed generally under the heads of equilibration, co-ordination of locomotion, emotional expression, and adaptive reactions in accordance with impressions made upon their organs of sense. These are organised in the mesencephalic and spinal centres in the highest degree in fishes, frogs, and pigeons; to a less degree in the lower mammals, and least of all in monkeys and man.

I do not intend on the present occasion to enter on a consideration of the respective *rôles* of the spinal, cerebellar, and mesencephalic centres in the regulation of these different forms of activity. We may—practically in some and theoretically in all—separate the mesencephalon and spinal cord into a congeries of individual centres, each with its own afferent and efferent nerves, co-ordinating synergic movements, each in its own province, and all co-operating together harmoniously by means of commissural or intracentral fibres. The individual metameres form units in a complex whole, acted on by the nerves of special sense, and subordinate to the supreme nerve centres, through which the adaptation of the organism to its environment is effected. Nor will I enter on a discussion of the vexed question as to whether the actions of the lower centres are indicative or not of intelligence. Most of the differences on this point turn mainly on the meaning of terms. If, with Mr. Romanes, we regard fluctuating adaptation to external conditions as the criterion of intelligence, we shall certainly not be able to deny that the actions of the lower centres are indicative of intelligence in this sense. For the observations of Steiner, Schrader, and others on the lower vertebrates, show that forms of activity, which we are accustomed to regard in man as exclusively cerebral, and indicative of conscious discrimination, are capable of being manifested by these animals in the entire absence of their cerebral hemispheres. Nor can we say that spontaneity, which we have also been accustomed to regard as conditioned by the cerebral hemispheres, is entirely abolished in brainless animals; for we see that, without any apparent change in external conditions, they move spontaneously, and comport themselves not unlike normal animals. We can, however, in most cases, if not in all, refer these so-called spontaneous movements to immediate ento- or epi-peripheral impressions; whereas, in normal animals, though their so-called spontaneity is primarily derived from a similar source, the connections are more remote and far more difficult to trace.

These and other similar facts lead to the conclusion that between the simplest reflex action and the highest act of intelligence there is no essential difference—each passing by insensible gradations into the other. We can infer only, we can prove nothing conclusively, regarding the existence of states of consciousness in others than ourselves, and less easily in the case of the lower animals than in man. But we are entitled to say that the activity of the lower centres does not affect the consciousness of the individual; for, when by lesion of the internal capsule the sensory tracts are cut off from their cortical connections, the individual has absolutely no consciousness of impressions made upon his organs of sense, so that we may conclude that, in man at least, states of consciousness are indissolubly connected with the activity of the cerebral hemispheres.

The results of ablation of the cerebral hemispheres indicate nothing for or against the doctrine of functional localisation, nor do the experiments of Goltz in the least degree militate against the existence of specific centres; for if, even after complete bilateral extirpation of these centres, the functions which survive do not transcend those capable of being manifested in the entire absence of the cerebral hemispheres, there still remains the question whether the lesions have not caused a loss or paralysis of something of a higher order. That this is so is capable of ample demonstration, of which not the least part has been contributed by the very facts which Goltz himself has ascertained through the numerous and varied devices which he has so ingeniously contrived. It is no explanation of the defects which admittedly result from removal of the cerebral hemispheres to say that they are caused by a loss of intelligence. This is merely restating the facts in a more metaphysical but less intelligible form. We are not, however, dealing with metaphysical terms when we are studying the effects of lesions of the cerebral cortex. We are dealing with material entities connected with sensory and motor tracts, and it is our object to determine, if possible, what are the anatomical and physiological factors which are co-related with the functions which we generalise under the head of intelligence; and there appears to be nothing which can, *a priori*, be urged against the notion that the various factors of intelligence have their substrata in definite regions specifically related to certain motor and sensory functions. Flourens, as is well known, denied every species of localisation in the cerebral hemispheres. To this conclusion he appears to have been led not more by his own experiments than by the prevalent conceptions as to the unity and indivisibility of the mind, and as a reaction against the organology of Gall and his followers. To Gall, however, let us in passing pay the tribute that in his analysis he followed strictly inductive methods, and made many observations of enduring value; though his synthesis of the brain as a congeries of separate organs, each autonomous in its own sphere, and all mysteriously inherent in some unifying, immaterial substratum, has failed to commend itself to the scientific world. Flourens thus sums up his conclusions:—

"Thus one may remove, anteriorly, or posteriorly, from above, or from the side, a considerable portion of the cerebral lobes without destroying their functions. Even a small portion of these lobes, therefore, suffices for the exercise of their functions. In proportion to the extent of the removal, all the functions become impaired, and gradually fail; and beyond certain limits they are altogether annihilated. The cerebral lobes, therefore, co-operate as a whole in the full and complete exercise of their functions. Finally, when one form of perception is lost, all are lost; when one faculty disappears, all disappear. There are, therefore, no special seats either of special faculties or special perceptions. The faculty of perceiving, judging, and willing one thing resides in the same region as that of perceiving, judging, and willing another; consequently, this faculty, essentially one, resides essentially in one organ."[19]

Though the doctrines of Flourens met with general acceptation, they were contested on experimental grounds by some physiologists, more particularly by Bouillaud.[20] The experiments of Bouillaud on pigeons, dogs, and rabbits led him to conclude that destruction of the anterior lobes alone caused symptoms of profound dementia. Though the animals were able to feel, see, hear, smell, and to execute a number of spontaneous and instinctive movements, they were unable to recognise their relations to the objects by which they were surrounded. They were unable to feed themselves, and had in general lost all reasoning powers. An animal, said he, in which the anterior lobes have been destroyed, "though deprived of the exercise of a more or less considerable number of intellectual acts, continues to enjoy its sensory faculties; a proof that 'sensation' and 'intellection' are not one and the same function, and that they have separate localities." Bouillaud's results have, I think, received confirmation and elucidation from my own experiments on monkeys, as well as those of Goltz

19 *Op. cit.*, p. 99.

20 "Rech. Expérim. sur les Fonctions du Cerveau, et sur celles de sa portion antérieure en particulier." *Journ. de Physiol. Expérim.*, 1830, T. x, p. 91.

and Schrader on dogs and pigeons. Bouillaud, however, did not consider that his own experiments had done more than merely raise the question of localisation, and it was generally believed that, so far at least as experimental data were concerned, the doctrine of specific localisation had no secure basis of support. From the clinical standpoint, however, facts were continually being presented which seemed altogether unintelligible except on some theory of localisation; and clinical observers, such as Bouillaud himself, Andral, and others, wisely suspended their judgment until further facts should be brought to light, which might serve to explain the apparent irreconcilable discrepancy between human pathology and experimental physiology.

Bouillaud[21] recorded certain clinical facts which seemed to indicate a connection between lesions of the anterior lobes and loss of speech, thus affording some confirmation of the theories of Gall on the subject. Dax (1836) established the special relation of aphasia to right hemiplegia and lesions of the left hemisphere; but the connection between aphemia, or aphasia, and lesion more particularly of a definite region of the left hemisphere, namely, the base of the third frontal convolution, was first pointed out by Broca (1861). Broca's observations have since been amply confirmed by clinical and pathological research, and further elucidated by physiological experiment.

The next great advance in cerebral localisation was made by Hughlings-Jackson (1861),[22] who, from a study of the forms of epilepsy, now appropriately known by his name, furnished cogent reasons for believing that certain convolutions near, and functionally related to, the corpus striatum had a direct motor signification. By irritation or "discharging lesions" of these convolutions, localised, or general unilateral convulsions of the opposite side of the body were induced. Owing, however, to the fact, as Hughlings-Jackson has remarked, that "the damage by disease is often coarse, ill-defined, and widespread," the determination of the functions of the brain by the clinico-pathological method had made comparatively little progress, there being apparently no constant uniformity between the seat of the disease and the symptoms manifested. The difficulty of discriminating between the direct and indirect effects of cerebral lesions has furnished Brown-Séquard[23] with arguments in favour of his peculiar views, that all

[21] *Archives de Médecine*, 1825.

[22] *Clinical and Pathological Researches on the Nervous System.*

[23] Physiological Pathology of the Brain, *Lancet*, 1876, and *Archives de Physiologie*, 1877-1890.

the symptoms of cerebral disease are due to some dynamic influence exercised by the lesion on parts situated at a distance (and always apparently out of reach), which are credited with the functions lost or otherwise disturbed.

A glance at the accompanying diagram (Fig. 2) founded by Exner[24] on the examination of a number of cases of lesion of the left hemisphere, will show you the extraordinary diversity in posi-

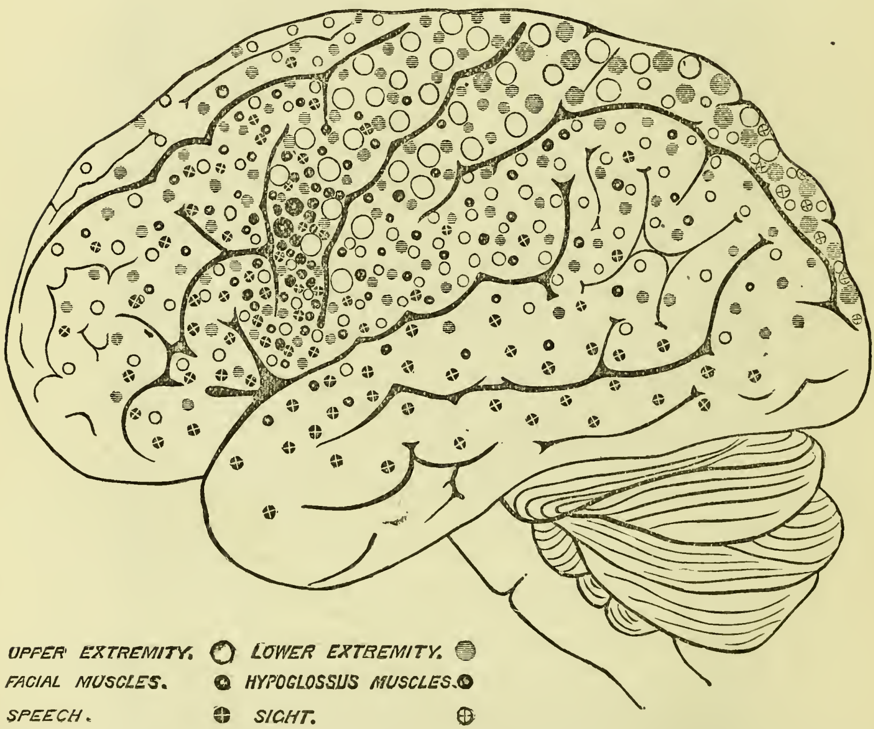

Fig. 2.—After Exner's Tafel xxv. The diagram is marked with larger and smaller circles of the same order. The larger circles indicate the absolute centres, the smaller the relative centres. The intensity of the latter is indicated by the closeness of the circles to each other.

tion of those accompanied by practically the same symptom. It will be seen, for instance, that though the lesions which cause affection of the upper extremity are mostly grouped in a certain region, yet there is scarcely a point on the convexity of the hemisphere lesion of which has not caused a similar result. These and

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[24] *Localisation der Functionen in der Grosshirnrinde des Menschen*, 1881.

such like are the data on which Exner has founded his theory of *absolute* and *relative* centres; absolute centres being those destruction of which invariably, relative centres being those destruction of which only frequently, induces the same symptom. The distinction appears to me to have no valid foundation. Mere frequency is not a sufficient basis on which to found causal relationship. For, if the so-called relative centres can be, and have been times out of number, destroyed without any disturbance of the function with which they are supposed to be related, and if the said function can be annihilated while the relative centres are intact, it is obvious that the relationship is nothing more than mere coincidence or juxtaposition.

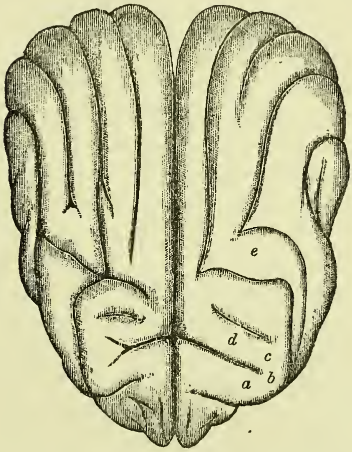

Fig. 3.—Centres of the brain of the dog according to Fritsch and Hitzig.

The whole aspect of cerebral physiology and pathology was revolutionised by the discovery, first made by Fritsch and Hitzig in 1870,[25] that certain definite movements could be excited by the direct application of electrical stimulation to definite regions of the cortex cerebri in dogs. As these experiments are now of historic interest, I extract the accompanying figure (Fig. 3) and the description, in their own words, of the facts which they had at that time ascertained.

"The centre for the neck-muscles (Fig 3 *a*) lies in the lateral part of the prefrontal gyrus at the point where the surface of this convolution abruptly descends. The outermost extremity of the

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[25] *Reichert, u. Du Bois-Reymond's Archiv*, 1870, Heft 3.

postfrontal gyrus contains, in the neighbourhood of the lateral end of the frontal fissure (Fig. 3 *b*) the centre for the extensors and abductors of the fore limb." Somewhat behind the same, and nearer the coronal fissure (Fig. 3 *c*) lie the ruling centres for the flexion and rotation of the limb. The centre for the hind leg (Fig. 3 *d*) is also found in the postfrontal gyrus, but nearer the middle line than that of the fore leg, and somewhat further back. The facial (Fig. 3 *e*) is innervated from the middle part of the super-Sylvian gyrus. This region generally has an extension of over 0.5 centimètre, and stretches before and behind the bend over the Sylvian fissure. We must add that we did not always succeed in getting the neck-muscles in action from the first mentioned point. The muscles of the back, tail, and abdomen we have often enough excited to contraction from points lying between those marked, but no circumscribed point from which they could be individually stimulated could be satisfactorily determined. The whole of the convexity lying behind the facial centre we found absolutely unexcitable, even with altogether disproportionate intensity of current."

The subject of the electrical excitability of the cortex and its signification was next taken up by myself in 1873,[26] more particularly with the object of putting to experimental proof the views of Hughlings Jackson in reference to the causation of unilateral epileptiform convulsions. While amply confirming these doctrines in all essential particulars, my attention became specially directed to the question of definite localisation, and I was led minutely to explore, not only the hemispheres of dogs, but also those of monkeys and various other orders of vertebrates. Similar researches have been undertaken and published in almost every country, and by experimenters too numerous to mention, but nowhere with greater care and detail than by Beevor, Horsley, and Schäfer[27] in our own. The facts revealed by electrical exploration of the hemispheres have been, and still are, the subject of considerable diversity of opinion, and by some, as Brown-Séquard,[28] are regarded as of no greater significance than the contortions which may be induced by tickling the sole of the foot. There cannot, however, be a doubt that from them, and the further experiments to which they have pointed the way, has sprung the whole modern doctrine of exact cerebral localisation.

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[26] Experimental Researches in Cerebral Physiology and Pathology, *West Riding Lunatic Asylum Reports*, vol. iii, 1873.

[27] *Phil. Trans.*, 1888.

[28] *Archives de Physiologie*, January, 1890.

Before discussing the different specific reactions and their functional significance, it will be desirable to enter on a brief consideration of the characters and conditions of the excitability of the cerebral cortex.

In normal states the grey matter of the cortex is entirely or almost entirely, insensible to mechanical stimulation. Luciani, however, states that though the convexity of the hemisphere does not react to this form of stimulation, yet he has been able to produce movements of the opposite limbs by irritation of the walls of the crucial sulcus. Couty[29] also states that he has found the convolutions mechanically excitable after ligature of the cerebral arteries. Whether we accept these statements as being strictly accurate or not, it is certain, as was shown by Franck and Pitres,[30] that when the cortex has become inflamed and congested by exposure or traumatic lesion, it becomes irritable to mechanical stimulation, and may respond not merely by partial movements of the opposite limbs, but also by a unilateral epileptic fit. This is, in fact, the experimental induction of the discharging lesions described by Hughlings Jackson. It is also held by some—for example, Landois[31]—that the cortex is chemically excitable: a fact, however, which may be due to the inflammatory condition of the tissues thereby induced. The most effective excitant is the application, by closely approximated electrodes, of a galvanic or faradic current of moderate intensity. Fritsch and Hitzig, in their researches, employed the former, but preference has generally been given by other experimenters to the faradic current as being the best calculated to elicit the characteristic reactions of the cortical centres. When an animal is sufficiently narcotised to abolish all restless or spontaneous movements—and the anæsthesia must not be too profound, otherwise all reactions cease—the application of the electrodes to different regions calls forth definite motor reactions with such uniformity that, when once the limits of the said region have been accurately defined, one may confidently predict the exact movement which will occur in animals of the same species. This is a fact which is beyond all dispute, and has been frequently demonstrated by myself, Horsley, and others, and, indeed, may be regarded as an ordinary lecture experiment.

Couty[32] is perhaps the only physiologist whose results appear

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29 *Comptes Rendus*, March, 1879.

30 *Archives de Physiologie*, 1883.

31 Abstract in *Neurolog. Centralblatt*, 1890, p. 145.

32 Le Cerveau Moteur, *Archives de Physiologie*, 1883.

to contradict the above statement; but as his experiments were performed on animals not narcotised, it is probable that any irregularity in the effects of excitation was due to spontaneous movements on the part of the animal. Some variations from absolute uniformity may, however, occur from want of symmetry in the convolutions, and still more from changes in the excitability of the cortex. These are particularly apt to occur after repeated exploration, so that a mixture of effects may be produced by diffusion of the current from the one centre into others which have been rendered hyperexcitable by previous stimulation. The lateral diffusion of the current, which always occurs more or less, is the chief obstacle to the precise delimitation of the cortical centres by the method of excitation. Hence the limits of a region may be somewhat differently given by different experimenters; but, making due allowance for all these sources of error, it has been found possible to arrive at a remarkable degree of harmony as to the locality and extent of the respective areas. The extrapolar diffusion of current which can be demonstrated in the brain, as in other animal tissues, has been regarded by Dupuy[33] as an insuperable objection to the theory that the results of application of the electrodes to the cortex are due to stimulation of the cortex itself; and attempts are made to explain them away by mere physical conduction of the currents to centres and tracts at the base of the brain. But no satisfactory explanation can thus be afforded of the manifest differences in reaction which follow the application of the electrodes to regions in close proximity to each other, nor of the total absence of reaction when the electrodes are placed on the island of Reil, which is nearer the base of the brain than other regions which act uniformly and without fail.

The chief objection to the direct excitability of the cortex itself is found in the fact that, even after removal of the cortex, similar reactions are still obtainable when the electrodes are placed on the subjacent medullary fibres. This was first pointed out by Burdon-Sanderson,[34] and has been confirmed by all subsequent experimenters. After removal of the cortex, however, the medullary fibres lose their excitability, like motor nerves separated from the anterior cornua of the spinal cord, so that, after a lapse of four days, no reactions can be produced by the strongest stimulation. This fact completely disposes of the physical-

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33 *Examen de quelques Points de la Physiologie du Cerveau*, 1873.
34 *Proceedings Royal Society*, June, 1874.

conduction-to-the-base-of-the-brain hypothesis. It has thus been satisfactorily established that the cones of medullary fibres, corresponding to the respective cortical centres, are functionally differentiated like the cortical centres themselves, and, as has

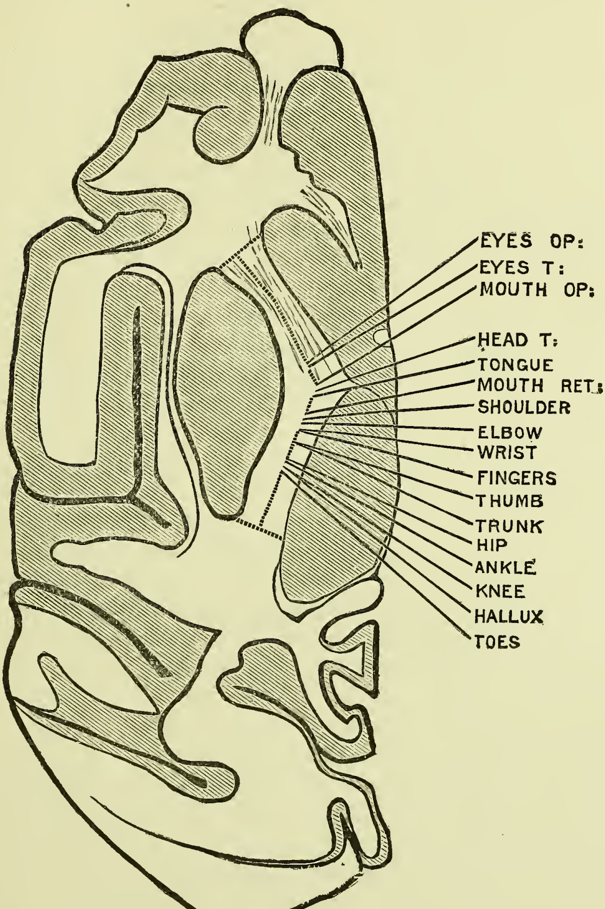

Fig. 4.—Arrangement of the motor fibres of the internal capsule, according to Beevor and Horsley.

been shown by Franck and Pitres,[35] and more recently, with greater detail, by Beevor and Horsley,[36] maintain their individu-

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[35] *Comptes Rendus de la Société Biolog.*, 1877.
[36] *Proceedings Royal Society*, No. 286, 1890.

ality, and are echeloned in definite and regular order in the internal capsule.

On the accompanying figure (Fig. 4), kindly supplied me by Dr. Beevor, are marked the points on the internal capsule from which, according to their recent researches, minimal stimulation excites the respective movements which are indicated on the margin. But it does not follow, because the medullary fibres are excitable, that the corresponding cortical regions are unexcitable, and that the current merely passes through them. It is *a priori* more likely that there is also functional differentiation of the cortical centres to which they are distributed, and that the grey matter is, under normal conditions, the natural excitant of the reactions which we are able to produce by artificial stimulation with the electric current. And a comparison of the respective reactions of the cortex and medullary fibres indicates such differences as can only be explained on the supposition that the cortical centres are themselves excitable.

First, as regards the relative excitability of the grey matter and subjacent medullary fibres. This is a point on which there are some differences of opinion, but Putnam found[37] the medullary fibres less excitable than the cortex, so that in order to produce the customary reaction, it was necessary to use a much stronger current than before. This has been confirmed by Franck and Pitres, who have further shown that the diminished excitability cannot be accounted for by mere shock or hæmorrhage, inasmuch as the neighbouring grey matter acted as readily as before. They have further given reasons for believing that the contrary results obtained by Richet,[38] and Bubnoff and Heidenhain[39] are due to the action on the cortex of the chloral and morphine under which their experiments were performed. These agents, without doubt, paralyse the excitability of the grey matter. It was noted by Fritsch and Hitzig, in their experiments, that the anodal closure was a more effective stimulus than the cathodal—a fact which might be interpreted as signifying that the real stimulus proceeded from the virtual cathode in the deeper layers of the cortex, or termination of the medullary fibres. This, however, has been shown by Gerber,[40] not to be uniformly

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[37] *Boston Med. and Surg. Journal*, 1874.

[38] *Sur les Circonvolutions Cérébrales*, 1879.

[39] *Pflüger's Archiv. f. Physiologie*, 1881.

[40] "Beiträge zur Lehre von der electrischen Reizung des Grosshirns," *Pflügers' Archiv für Physiologie*, Band 39, 1888.

the case. Gerber finds that when the cortex is in a normal state the cathode is the more effective stimulant, but that when changes have occurred from long exposure the anode predominates. These experiments would, therefore, indicate that in the normal condition of the brain the laws of galvanic excitability are the same as for motor nerves.

Another important difference between the reactions of the cortex and the subjacent medullary fibres, which was first pointed out by Franck and Pitres, is that the time lost between the application of the stimulus and the occurrence of muscular contraction is much greater in the case of the former than the latter. This interval, after deducting the time necessary for the transmission of the impulse through the spinal cord and motor nerves, indicates a retardation in the cortex of 0.045 second. After removal of the grey matter and application of the electrodes to the medullary fibres, the period of retardation diminishes to 0.030 second, that is, about one-third less, and this difference is put at a considerably higher figure by Bubnoff and Heidenhain.

The signification of this fact is that the grey matter of the cortex does not behave like an inert layer, which merely allows transmission of the electric current to the medullary fibres, but, like other nerve centres, stores up and transforms the stimuli which it has received into its own energy.

There is also a characteristic difference between the muscular curves registered on stimulation of the cortex and medullary fibres respectively. In the latter case the curve rises abruptly, and is of short duration; while in the former it rises more gradually, is more prolonged, and frequently marked by the occurrence of a secondary tetanus, which latter is altogether peculiar to the cortex, and is never seen when the medullary fibres alone are stimulated. The cortex is apt, after repeated stimulation, or after the receipt of a succession of stimuli each insufficient to produce reaction, to respond by tonic, followed by clonic, spasms of the correlated muscles of a truly epileptic type. These convulsions tend to spread and become generalised in the order and sequence originally described by Hughlings Jackson. They never occur on stimulation of the medullary fibres alone, apart from the intervention of the grey matter of the cortex on the one side or the other, and cannot be produced if the cortical centres are entirely destroyed on both sides. The duration of the effects of stimulation of the medullary fibres is strictly proportional to that of the stimulus which is applied to them. We shall also see as we proceed that the effects of localised destruction of the cortex are the counterpart of those of irritation, however induced, and we may from this conclude that there is the same functional differentiation in the cortex as in the medullary fibres, even if the facts which I have just mentioned should not be regarded as of themselves completely establishing this proposition.

LECTURE II

LECTURE II.

Mr. President and Gentlemen,—I will now invite your attention to a brief consideration of the phenomena of electrical irritation of the brain of the monkey, more especially as determined by my own experiments, and those of Horsley, Schäfer and Beevor, which, though in all essentials confirming mine, have been worked out with more elaborate detail and minuteness.[1]

Beginning anteriorly we find that what is generally termed the prefrontal lobe—that is, all in advance of a line drawn at right angles to the anterior extremity of the precentral sulcus—gives no, or very doubtful, response to electrical stimulation.

Between this line and that of the precentral sulcus continued upwards to the longitudinal fissure, there is a region or area (1, 2, Fig. 5; Figs. 6 and 7, head), stimulation of which causes opening of the eyes, dilatation of the pupils, and movements of the head and eyes to the opposite side. This area has been further differentiated by Beevor and Horsley, according to the primary movements which result from minimal stimulation of the points indicated on their diagram (Fig. 8). The corresponding region in the brain of the dog is (12, Fig. 9). No similarly differentiated centre is seen in the cat (Fig. 10) or rabbit (Fig. 11).

At the upper extremity of the central convolutions (ascending frontal, ascending parietal, and postero-parietal lobule) (1, 2, Fig. 5; leg, Figs. 6 and 7), and extending over the margin of the hemisphere into the posterior part of the marginal convolution, or paracentral lobule, electrical stimulation causes movements of the *lower extremity.* The movements vary according to the position of the electrodes on this area. Behind the fissure of Rolando the movements are chiefly, or exclusively, of the foot or toes. Anterior to the fissure of Rolando they are combined with flexion of the

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[1] Horsley and Schäfer, *Phil. Trans.*, B. 20, 1888; Beevor and Horsley, *Phil. Trans.*, B. 1890.

leg and thigh. With minimal stimulation the movements may be still further differentiated (Fig. 8), and, in particular, the great toe can be excited to movement separately by stimulation at the upper extremity of the fissure of Rolando. The corresponding region in the brain of the dog, cat, and rabbit, is indicated by 1, Figs. 9, 10, 11.

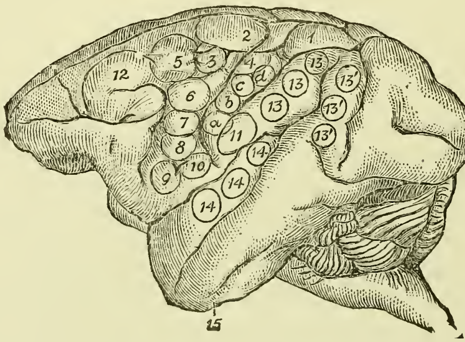

Fig. 5.—The left hemisphere of the monkey. 1. The opposite hind limb is advanced as in walking; 2, flexion with outward rotation of the thigh, rotation inwards of the leg. with flexion of the toes; 3, the tail; 4, the opposite arm is adducted, extended, and retracted, the hand pronated; 5, extension forwards of the opposite arm; *a, b, c, d,* movements of fingers and wrist; 6, flexion and supination of the forearm; 7, retraction and elevation of the angle of the mouth; 8, elevation of the ala of the nose and upper lip; 9 and 10, opening of the mouth, with protrusion (9) and retraction (10) of the tongue; 11, retraction of the angle of the mouth; 12, the eyes open widely, the pupils dilate, and head and eyes turn to the opposite side; 13 and 13′, the eyes move to the opposite side; 14, pricking of the opposite ear, head and eyes turn to the opposite side, pupils dilate widely.

Below the leg area, and partly in front of it, and occupying the middle third, or rather two-fourths of the central convolutions, there is a region stimulation of which causes movements of the upper extremity (3, 4, 5, 6, *a, b, c, d,* Fig. 5, and arm, Fig. 6). In this area it is possible to differentiate, more or less completely, movements of the upper arm (protraction and retraction); movements of the forearm (flexion, supination, etc.); and of the wrist, fingers and thumb. The proximal movements are represented most in the upper part of this region; the distal movements, that is, those of the fingers and thumb, most at the lower part.

By minimal stimulation at the lower extremity of the intraparietal sulcus the thumb may be individually thrown into the action (Fig. 8). The corresponding region in the brain of the dog is that indicated by the numerals 4 and 5 situated on the post-crucial division of the sigmoid gyrus (Fig. 9), and by the same numerals on the brain of the cat (Fig. 10), together with *a* situated on the anterior extremity of the second external convolution. Stimulation of this latter point causes protrusion of the claws; an action comparable to the movements of the wrist and fingers excited from the lower part of the ascending parietal convolution in the monkey. The corresponding region in the brain of the rabbit is indicated by the same numerals (4, 5, Fig. 11).

Below the arm area, and occupying the lower third of the central convolutions, there is a region stimulation of which causes movements of the face, mouth and tongue. In the upper part of this area can be differentiated centres for movements of the upper facial muscles (7, 8, Fig. 5) in front of, and platysma (11) behind the fissure of Rolando. The corresponding region in the brain of the dog, relatively much larger than in the monkey, is indicated by the numerals (7, 8, Fig. 9), and the same indicate the homologous regions in the brain of the cat (Fig. 10), and rabbit (Fig. 11). In the lower portion excitation causes movements of the mouth and tongue; protrusion of the tongue being generally caused by stimulation anteriorly (9, Fig. 5), and retraction by stimulation posteriorly (10, Fig. 5).

It has further been demonstrated by Semon and Horsley [2] that excitation of the lower extremity of the ascending frontal convolution causes phonatory closure of the vocal cords. The phonatory closure of the vocal cords was first demonstrated ocularly in the dog, on irritation of the pre-sigmoid region, by Krause,[3] though I had many years previously,[4] given audible demonstration of the same fact by showing that stimulation in this neighbourhood not infrequently caused barking; and similar effects (spitting, mewing) by stimulation of the homologous region in the brain of the cat. I also pointed out that the movements occurring on stimulation of this part were distinctly bilateral, an effect which Krause, Horsley and Semon, have found to be true also of movements of the vocal cords.

The areas for the head and eyes, arm and leg, extend over the margin of the hemisphere into the mesial aspect or marginal convolution. These I had to some extent noted in my first experiments, but a more thorough exploration of the reactions of this

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[2] On the Central Motor Innervation of the Larynx, BRITISH MEDICAL JOURNAL, December 21st, 1889.

[3] *Pflüger's Archiv.*, 1883.

[4] *West Riding Asylum Reports*, 1873.

region was first made by Horsley and Schäfer.[5] Excitation of this convolution from before backwards (see Fig. 7), causes movements of the spine, tail, and pelvis; behind these, extension of the hip, flexion of the leg, and lastly, movements of the foot and toes. These movements are not, however, always clearly differentiated, as they are apt to run into each other, and to be complicated by secondary movements of the various segments of the limb.

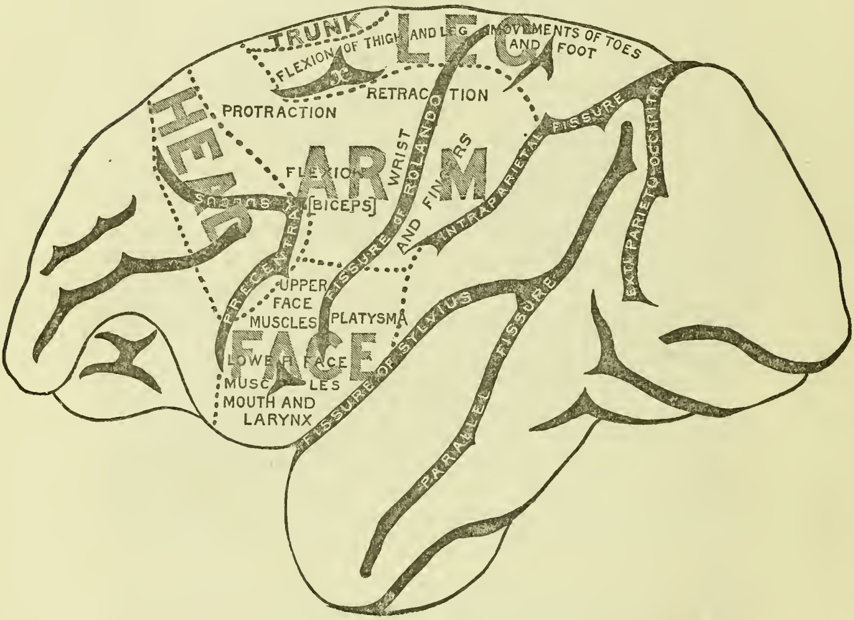

Fig. 6.

Stimulation of the angular gyrus, *pli courbe* (13′ 13, Fig. 5), causes movements of the eyeballs, and occasionally of the head, to the opposite side, generally combined with an upward or downward direction, according as the electrodes are on the anterior or posterior limb of this gyrus. The condition of the pupils is not constant, occasionally they are contracted. The corresponding region in the brain of the dog is indicated by 13 (Fig. 9), situated on the second external convolution, and the homologous region in the brain of the cat (Fig. 10), and the rabbit (Fig. 11), is indicated by the same numerals.

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[5] *Phil. Trans.*, vol. 179, 1888.

Excitation of the occipital lobe appeared in my earlier experiments to yield negative results. But Luciani and Tamburini[6] occasionally obtained movements of the eyeballs similar to those occurring on excitation of the angular gyrus, though less marked And Schäfer[7] describes similar movements as occurring from stimulation of different parts of the occipital lobe and neighbouring regions. My own experiments on several monkeys, though not opposed to those of Schäfer, are more in harmony

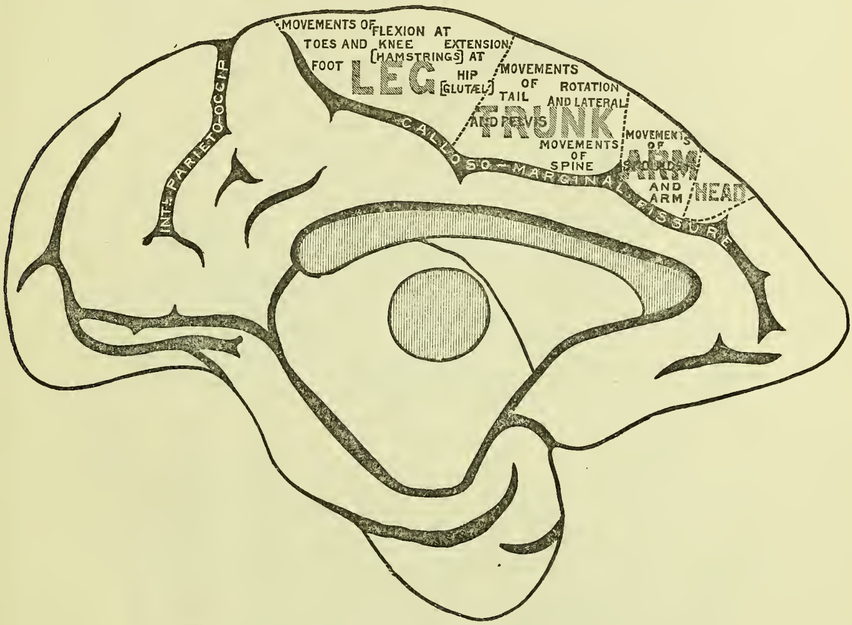

Fig. 7.—The motor areas according to Horsley and Schäfer.

with those of Luciani and Tamburini, and show that, though movements of the eyeballs may be obtained by excitation of the occipital lobe, they are, as a rule, less constant and less easily excited than from stimulation of the angular gyrus.

Stimulation of the superior temporal gyrus (14, Fig. 5) causes pricking of the opposite ear, opening of the eyes, dilatation of the pupils, and direction of the head and eyes to the opposite side. Precisely the same reaction occurs after stimulation of the posterior limb of the third external convolution of the brain of the dog

6 *Sui Centri Psico-Sensori Corticali*, 1879.
7 *Proc. Roy. Soc.*, 1888.

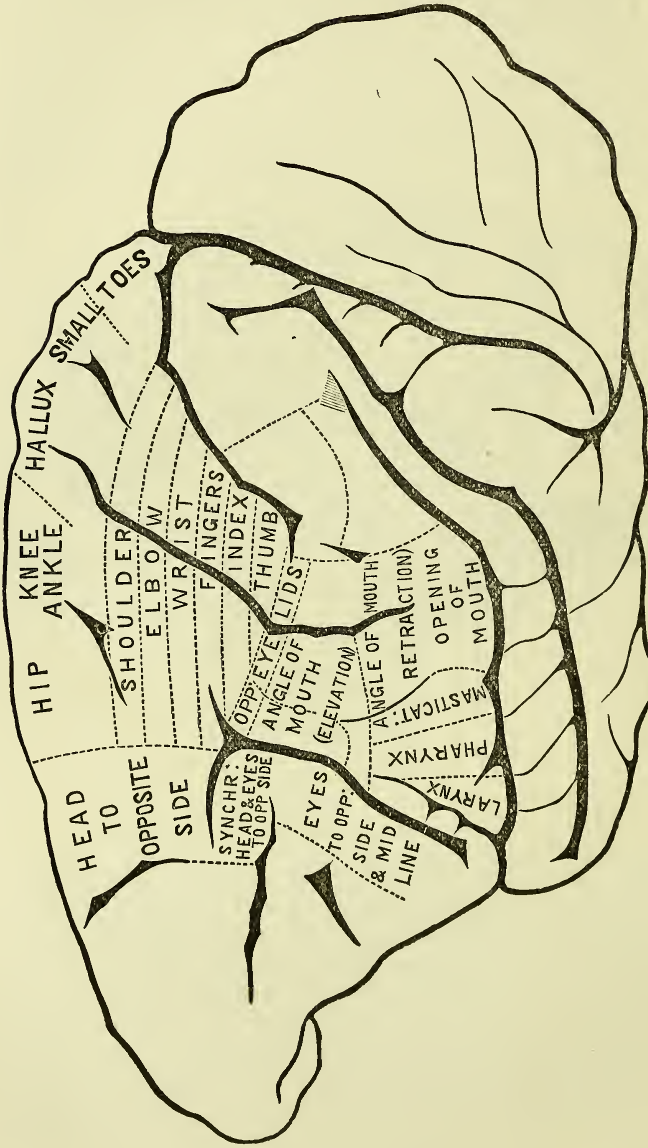

Fig. 8.—Motor areas according to Beevor and Horsley.

(14, Fig. 9), and so also in the brain of the cat (Fig. 10), and homologous region of the brain ofthe rabbit (Fig. 11). Sometimes only movements of the ear are caused, and sometimes the animal attempts to bound off the table as if suddenly startled.

Stimulation of the hippocampal lobule or anterior extremity of the hippocampal gyrus in monkeys, dogs, cats, and rabbits causes precisely the same results—namely, torsion of the nostril on the same side—as if from irritation applied directly to the nostril itself. Irritation of the gyrus hippocampi occasionally caused movements such as might be conditioned by direct irritation of the opposite limbs; but beyond this I have not been able

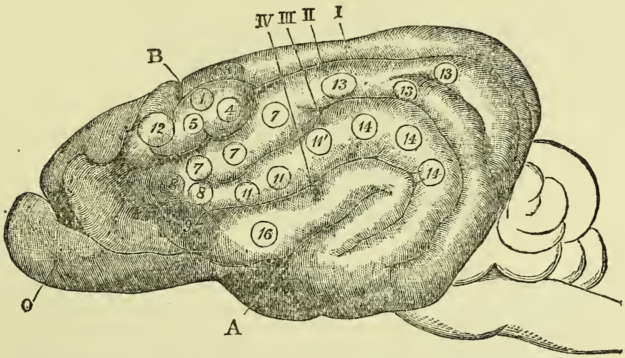

Fig. 9.—Left hemisphere of the brain of dog. 1. The opposite limb is advanced; 3, lateral or wagging motion of the tail; 4, retraction with adduction of the opposite fore limb; 5, elevation of shoulder, and extension forwards of the opposite fore limb; +, flexion of the paw; 7, action of the orbicularis oculi and zygomatics; 8, retraction and elevation of the opposite angle of the mouth; 9, opening of the mouth and movements of the tongue; 11, retraction of the angle of the mouth; 12, the eyes widely opened with dilatation of the pupils, with movement of the eyeballs and head to the opposite side; 13, movement of the eyeballs to the opposite side; 14, pricking, or sudden retraction, of the opposite ear; 15, torsion of the nostril on the same side.

to obtain any constant reaction from stimulation of the rest of the temporal lobe or other portions of the cortex.

Such is briefly a summary of the phenomena of electrical irritation of the different regions of the cerebral cortex. These results, apart from the interpretation which we put upon them, indicate some form of functional differentiation; and it is obvious, on comparing the corresponding areas in the brain of the monkey, dog, cat, and rabbit, that there are great differences as regards their relative extent, and the character of the movements with which they are in relation. Whether complete parallelism obtains

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between the brain of the monkey and the brain of man is a question which, until recently, could only be answered by reference to the facts of localised lesions. Bartholow[8] and Sciamanna[9] had observed movements of the opposite side of the body on stimulation of the cortex through the dura mater—the former in a case of cancerous ulceration and the latter in a case of trephining. But their results, though so far in accordance with those of experimentation on monkeys, were lacking in precision. Recently, however, surgeons have on several occasions resorted to gentle faradisation of the cortex, in order to define accurately the regions which they have desired to extirpate for the cure of focal

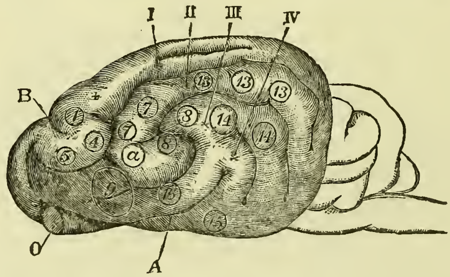

Fig. 10.—Left hemisphere of the brain of the cat. 1. Advance of the opposite hind limb; 4, retraction and adduction of the opposite foreleg; 5, elevation of the shoulder, with flexion of the forearm end paw; A, clutching or grasping action of the paw, with protrusion of the claws; 7, elevation of the angle of the mouth and cheek, with closure of the eye; 8, retraction, with some degree of elevation of the angle of the mouth, and drawing downward and forward of the ear; 9, opening of the mouth and movements of the tongue; 13, the eyeballs move to the opposite side; 14, pricking of the ear, and head and eyes turn to the opposite side; 15, elevation of the lip and torsion of the nostril on the same side; divergence of the lips.

epilepsy. One of these has been reported by Horsley, and several others have been quoted by Mills in his valuable memoir on Cerebral Localisation in its Practical Relations.[10] In one case the lower halves of the two central convolutions—the posterior extremity of the second frontal and the posterior superior corner of the third frontal convolution—were exposed in the left hemisphere. "Careful examinations were made with the faradic current applied to the cortex with the view of locating the proper centres for excision. Four distinct responses in the shape of

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[8] *Amer. Journ. Med. Sciences*, April, 1874.

[9] *Arch. di Psichiatria*, 1882.

[10] Read before the Washington Congress, September 19th, 1888; reprinted in *Brain*, 1889.

definite movements were obtained after several trials; these were (1) in the most anterior position at which movements resulted, distinct conjugate deviation of the head to the opposite side; (2) a little below and behind this point, drawing of the mouth outwards and upwards; (3) above this spot for movements of the angle of the mouth, about half an inch, extension of the wrist and fingers was produced; (4) behind and above the latter point, distinct flexion of the fingers and wrist. Continuing and increasing the faradic application at this last determined point, the fingers, thumb, wrist, and forearm were successively flexed, and the whole extremity assumed the 'wing-like' position. The order of events, according to three persons who were present, and who observed the patient's spasms, being exactly that which had been noticed at the beginning of his convulsive seizures."

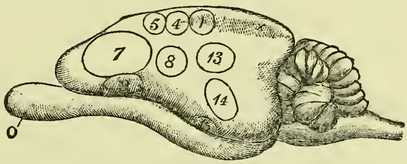

Fig. 11.—Left hemisphere of the brain of rabbit. 1. Advance of the opposite hind leg; 4, retraction with adduction of the opposite fore limb; 5, elevation of the shoulder and extension forward of the fore limb; 7, retraction and elevation of the angle of the mouth; 8, closure of the opposite eye; 9, opening of the mouth, with movements of the tongue; 13, forward movement of the opposite eye, occasionally turning of the head to the opposite side; 14, sudden retraction and elevation or pricking of the opposite ear; 15, torsion or closure of the nostril.

In a second case reported by Keen:[11] "On touching the cortex with the electrodes at a position which apparently corresponded to the anterior portion of the pre-Rolandic convolution, just behind the precentral fissure, movements of the wrist and fingers were produced. The hand moved in extension in the mid-line and to the ulnar side at different touches, the fingers being extended and separated. Above the region in which these movements were obtained application of the current caused movement of the left elbow, both flexion and extension, and of the shoulder, which was raised and abducted. Below the region, where the hand movements were excited, the application of the current produced an upward movement of the whole of the left face." These results correspond very closely with the position of the various centres as already defined.

[11] *Amer. Journn. Med. Sciences*, November, 1888.

In another case, reported by Lloyd and Deaver,[12] an area was exposed in the right hemisphere corresponding to the junction of the middle and lower thirds of the central convolutions. When the electrodes were applied to a point just posterior to the fissure of Rolando the movements which occurred were in order—flexion of the thumb on the palm, flexion of the fingers, flexion of the wrist, extending to flexion of the elbow. At a point in front and below stimulation caused contraction of the facial muscles of the opposite side.

In a fourth case, reported by Nancrede,[13] movements of the thumb were induced by stimulation of a region corresponding to the second lower fourth of the ascending parietal convolution. All these results are in close harmony with those obtained on stimulation of the cortex of the brain of the monkey, and we have therefore every reason to believe that, *cæteris paribus*, the functional relations of the human cortex are identical with those of the lower animals.

So far as the excitation method is concerned, we are entitled to say that, whether the individual segments of a limb are separately localised, or are represented, more or less, throughout a common area, the areas as a whole are completely differentiated from each other. No movements of the leg result from irritation of the facial centres, nor of the face from the leg centres. The face area and leg area are thus entirely differentiated from each other, and from the oculo-motor area. What is true of centres widely apart is doubtless true of centres which are in close proximity to each other. The fact that stimulation of the margin of a given area is apt to produce joint movements of this and the adjoining area must not be taken to imply that this portion subserves conjoint functions—say of the arm and leg, or arm and face.

The true explanation appears to me to be that the excitation method is unable completely to differentiate the boundaries of the respective centres. Regions which are in the closest proximity to each other, anatomically and functionally, are apt to be discharged together by diffusion of the stimulus. Nor, even if we are unable to entirely dissociate the centres from each other by the destructive method, are we on this ground entitled to conclude that there is any functional fusion between the two; for a destructive lesion, however small, situated on the margin of any given centre, is calculated to affect the functions of more than one. Facts will be

12 *Amer. Journ. Med. Sciences*, November, 1888.
13 *Medical News*, November 24th, 1888.

adduced as we proceed which to my mind justify the conclusion that the areas as a whole are as completely differentiated from each other as the limbs themselves, or one organ of sense from another.

We have seen, however, in respect to the individual movements of a limb, that though one particular movement can frequently be isolated by minimal stimulation of a definite point within the general area, yet the same movement may occur along with others when another part of the area is under stimulation. This may be interpreted either on the supposition that the particular movement, say of the thumb, is represented throughout the whole of the arm area, or that it is only a case of diffusion of the stimulus from one part to another. It is difficult to decide which of these views is the correct one, and it may be that neither accurately represents the whole truth. For the reactions of the limbs which result from stimulation of the cortex are not mere muscular contractions, but synergic movements co-ordinated into acts; and inasmuch as has been shown by Professor Yeo and myself,[14] the same muscles or muscular groups enter into the composition of the different movements innervated by the respective motor roots of the brachial and crural plexuses, so the same muscular groups may have a multiple representation in the various subdivisions of the general area. And it would appear that in the cortical areas there is a much greater differentiation than in the respective segments of the brachial and crural enlargements of the spinal cord. But in my opinion any further multiple representation outside the general area of a limb is altogether opposed to the facts of localisation as determined either by the methods of excitation, or destruction, or both.

We have next to inquire into the important and much disputed question as to the signification of the motor reactions which result from electrical stimulation of the different cortical regions. Though many of the movements are evidently such as may be termed purposive, it does not follow that they are indicative of direct stimulation of motor regions in the strict sense of the term, for the movements may be the result of some psychical condition incapable of being expressed in physiological terms; or they may be reflex, and thereby not differing essentially from those resulting from peripheral stimulation; or they may be motor in the sense of being due to irritation of parts in direct connection with

[14] *Proc. Roy. Soc.*, 1881, The Functional Relations of the Motor Roots of the Brachial and Lumbo sacral Plexuses.

the motor tracts and motor nerves, or they may be partly one and partly the other. The method of excitation itself is not competent to solve these questions, and requires as a complement the strictly localised destruction of those areas, stimulation of which gives rise to definite motor reactions.

A careful consideration of the reactions in different orders of animals, and the fact that similar movements are in some cases excitable from different cortical regions, led me to believe that they might have various significations, and I formed the hypothesis that some might be due to stimulation of motor regions proper, while others might be looked upon as the associated expression of subjective sensation. On this hypothesis I instituted localised destructive experiments, and thus determined the existence of sensory or perceptive centres respectively related to the different forms of sensibility, as well as of centres more especially, if not exclusively, motor in character. The existence of distinct sensory centres has been confirmed by succeeding physiological and clinical research, and I have the satisfaction of thinking that such errors as I have committed in the delimitation of the various sensory regions have been errors more of omission than of commission, and that the localities in which I originally fixed the respective sensory areas correspond in part at least with the position assigned to them by the most reliable experimental and clinical methods.

The Visual Centres.—I will first call your attention to the reactions occurring on stimulation of the occipito-angular region in monkeys, and its homologue in the lower orders of animals. The reactions, as we have already seen, are movements of the eyeballs, and occasionally of the head to the opposite side; and frequently also of the pupils, not always uniform in character, being sometimes contraction, at other times dilatation. These movements I have found to be most easily and most uniformly excited from the anterior and posterior limbs of the angular gyrus. As a rule, along with the lateral movements there is upward direction when the anterior limb, and downward when the posterior limb of this gyrus is excited. Movements of the eyeballs are also obtainable, as Luciani and Tamburini first pointed out, from irritation of the occipital lobe. Schäfer, who omits the anterior limb of the angular gyrus, though I have found this as excitable as the rest, obtains downward movements of the eyes on stimulation, not only of the posterior limb of the angular gyrus, but also of the upper end of the middle temporal gyrus, that part of the occipital lobe immediately behind the external parieto-occipital fissure, and on each side of the internal parieto-occipital fissure. He obtains upward movements on stimulation of the under surface of the occipital lobe, the lower part of the mesial aspect of this lobe, and of the lower margin of the convex surface. He obtains a simple lateral movement of the eyes on excitation of the rest of the convex aspect of the occipital lobe and a narrow strip of the mesial surface along the margin of the great longitudinal fissure. The middle portion of the mesial surface does not appear to be included in this scheme.

My hypothesis that these movements of the head and eyes are the signs of the arousal of subjective visual sensation, and due to associated action of the frontal or subcortical oculo-motor centres, has received confirmation from the experiments of Schäfer on the latency periods of the ocular movements following excitation of the frontal and occipito-temporal regions respectively.[15] The result of this comparison made in a number of monkeys was to show that the latent period is longer by some hundredths of a second in the case of stimulation of the occipital lobe than of the oculo-motor centre of the frontal area; thus indicating that in the former case the nervous impulses must be transmitted through at least one more nerve centre than in the latter. This would agree with the hypothesis that in the one case the movements were reflex, and in the other direct. The fact that the ocular movements are still obtainable on stimulation of the occipito-angular region, after complete removal of the frontal regions, shows that they are not necessarily indicative of the associated action of these cortical centres, but may be due, if they are not always so, to excitation of the oculo-motor centres of the corpora quadrigemina.

Danillo[16] has found that severance of the fibres of association between the occipital lobe and the frontal region does not prevent the occurrence of the ocular movements; while Bechterew[17] and Munk[18] have found that the movements are entirely annihilated by severance of the subjacent medullary fibres. It is contended by Danillo and Bechterew that the movements cannot, therefore, be regarded as indicative of subjective visual sensation; but this would not be disproved even if the movements still continued

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15 *Proc. Roy. Soc.*, February 13th, 1888.
16 *Archives de Neurologie*, vol. xviii, 1889, p. 145.
17 *Neurolog. Centralblatt.*, September 15th, 1889.
18 *Sitzungsberichte der Akad. d. Wiss. zu Berlin* vol. xvi, January, 1890.

after removal of the grey matter, for the excitation of the medullary fibres would be equivalent to excitation of the cortex itself. We may assume with Munk that there are radial or centrifugal fibres between the occipital cortex and the oculo-motor centres; and that excitation of the central expansion of these tracts would produce practically the same effect as stimulation of the centres with which they are in relation.

The occipito-angular region is the visual area of the cortex. Complete destruction of this area in the one hemisphere causes permanent hemianopia to the opposite side by paralysis of the corresponding halves of both retinæ; while bilateral destruction causes complete and enduring blindness of both eyes. Apart from the loss of vision, there are no other sensory or motor defects. The sensibility of the eyeball is intact, and the ocular movements are absolutely unimpaired. There is no impairment of the sensibility or motor power of the limbs. The other special senses are unaffected. If the destruction of the occipito-angular region is incomplete, unilaterally or bilaterally, the resulting hemianopia in the one case is not enduring, nor is the blindness permanent in the other.

There is, however, scarcely a particular of the above general statement which has not been controverted; but I am of opinion that every one of them is in accordance with the evidence furnished by strictly localised and carefully observed lesions of this region.

In my earlier investigation, I was led to believe that the angular gyri alone constituted the visual centres, a conclusion which I founded on the positive effects of lesions of the angular gyri and the uniformly negative results of destruction of both occipital lobes, except when the lesions trenched on the parieto-occipital fissure. In the latter case it appeared to me that the imperfections of vision or occasional total blindness were due to interference with the functions or the connections of the angular gyri themselves. I show you here a photograph of the brain of one of my earlier experimental animals.[19] Both occipital lobes were removed at the same time. Some encephalitis ensued, which caused extension of the primary lesions. You will see that on the right side, not only the occipital lobe, but also part of the posterior limb of the angular gyrus has been removed. On the left side the angular gyrus is intact, superficially, but the

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[19] Experiment XXIV, *Phil. Trans.*, vol. clxv, part 2, 1875.

medullary fibres of the cut surface bulge considerably, owing to inflammatory hernia. Notwithstanding this extensive bilateral lesion, the animal, within an hour of the operation, gave clear evidence of the retention of vision; for it made grimaces, and ran away when threatened. Subsequent examination revealed the fact that vision, though good, was impaired, as indicated by some want of precision in laying hold of objects offered it. But, beyond this slight defect in vision, there was no impairment of the animal's faculties in other respects, and it continued well until its death after a second operation three weeks subsequently, in which the greater part of both frontal lobes were removed. This second operation caused no further impairment of the animal's vision—a fact of great importance in reference to the question of the relation of the frontal lobes to the sense of sight.

Inasmuch as in this animal, as well as in others, in which similar symptoms occurred, the lesions implicated the region of the parieto-occipital fissure and angular gyrus, I attributed the impairment of vision to this cause; for, when the line of section of the occipital lobes was well separated from this fissure, no impairment of vision was perceptible. Thus the occipital lobes were exposed on both sides in a monkey, and the surface destroyed by the cautery, which was also passed deeply into the interior of the lobes so as to break up the medullary fibres. The operation was completed at 3 30 P.M. The following are the notes of the animal's condition:—

"4.10 P.M. The animal, after lying in a state of stupor till now, begins to move, but staggers a good deal. The eyes are open and the pupils dilated. It indicated consciousness by turning its head when called to.

"5.45 P.M. Gives emphatic evidence of sight. Ran away when I approached it, carefully avoiding obstacles. Seeing its cage door open, it entered and mounted on its perch, carefully avoiding the cat which had taken up its quarters there. Tried to escape my hand when I offered to lay hold of it, but picked up a raisin which I had left on the perch."[20]

Notwithstanding the extensive destruction of both occipital lobes in this case, the animal, in a little more than two hours after the operation, gave the most emphatic evidence of precise vision.

In another case in which the occipital lobes were severed by a

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[20] Experiment XXII, *Phil. Trans.*, vol. clxv, part 2, p. 25.

perpendicular section a quarter of an inch posterior to the parieto-occipital fissure,[21] the animal, notwithstanding the removal of at least two-thirds of both occipital lobes, gave clear evidence of vision within half an hour after the operation. In another monkey in which my colleague, Professor G. F. Yeo, removed about two-thirds of both occipital lobes, the animal within two hours after the operation was able to pick up minute objects lying on the floor.[22]

I show you here also a photograph of the brain of a monkey in which the left occipital lobe was removed by an incision immediately posterior to the parieto-occipital fissure. In this case, owing to the dressings having been torn off, the wound became septic and the animal died on the fifth day. On the day after the operation, however, no imperfection of vision could be discovered; for the animal took things offered it on the right or left front, and was able to run about the laboratory in every direction, passing among chairs and other articles of furniture without ever once knocking its head on one side or the other—actions which were altogether inconsistent with the existence of hemianopia.

You will see that the margin of the plane of section, which bulges considerably from hernial protrusion, corresponds nearly with the external parieto-occipital fissure.[23] These experiments illustrate the negative effects of unilateral and bilateral lesions of the occipital lobe. I had found, however, in my earlier experiments that destructive lesions of the cortex of the angular gyrus on the one side caused temporary complete loss of vision in the opposite eye, so that the animal responded to no test of vision, and, when urged to move, ran blindly against every obstacle in its path,[24] and that, when both angular gyri were similarly destroyed, complete blindness ensued in both eyes.[25]

The following observations were made on a monkey whose angular gyri were destroyed on both sides with the galvano-cautery. It was at once let loose, but appeared scared, and would not stir from its place. It was therefore for some hours impossible to obtain any satisfactory information as to its powers of vision. The pupils were contractile to light, and a light flashed in the eyes caused some wincing. When a piece of apple was

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[21] Experiment XXIII, *Phil. Trans.*, *sup. cit.*

[22] Experiment IX, *Phil. Trans.*, 1884.

[23] See Fig. 1, Plate 20, *Phil. Trans.*, part 11, 1884.

[24] See Experiments VII, VIII, IX, *Phil. Trans.*, vol. clxv, 1875.

[25] Experiment X, *op. cit.*

dropped near it, so as to come in contact with its hand, it took it up, smelt it, and ate it with signs of satisfaction. Hearing was acute, and it turned its head and replied when called to by name. With the exception of reluctance to move from its position, arising evidently from a sense of insecurity, there was nothing to indicate decisively that the animal was blind. But I had found that this animal was very fond of sweet tea, and would run anywhere after it. I therefore brought a cup of sweet tea, and placed it to its lips, when it drank eagerly. The cup was then withdrawn and placed in front of it, a little distance, but the animal, though from its gestures intensely eager to drink further, was unable to find the cup, though its eyes were looking straight into it. This test was repeated several times, and with exactly the same result. At last, on the cup being placed to its lips, it plunged its head in, and continued to drink till every drop was exhausted, while the cup was lowered and drawn half way across the room. Next day the animal still continued blind, and paid no attention to threats, grimaces, or other means of appeal to its sense of vision. It was then killed, in order that the position and extent of the lesions might be accurately determined before secondary inflammatory processes could have advanced. These had already begun, but were confined to the angular gyri, which were somewhat swollen and raised, and to the adjoining anterior margin of the occipital lobes, and with slight implication of the posterior margin of the left ascending parietal convolution. The destruction was purely cortical, the grey matter alone being disorganised, and on the angular gyri exclusively.

These facts seemed to me to justify the opinion that the angular gyri were the visual centres, each being in relation with the whole of the opposite eye, since the effect of unilateral extirpation was for the time total blindness of the opposite eye, and not hemiopia. And it further seemed as if the rapid recovery from unilateral lesion were due to the compensatory action of the other gyrus; inasmuch as bilateral destruction caused total blindness in both eyes of a more enduring, and, as I ventured to suppose, probably permanent, nature. But further investigation on animals kept alive for much longer periods than were compatible with the exact limitation of the lesion under old surgical methods showed that this conclusion was erroneous. My later investigations, in conjunction with Professor Yeo, under strictly antiseptic precautions, proved that the results of unilateral and bilateral extirpation of the angular gyrus, though entirely in harmony with my previous researches, were more temporary than I had previously thought, and that bilateral destruction did not cause permanent total loss of vision.[26] In illustration I would quote the details of the following experiments.

In one animal the left angular gyrus was cauterised with the galvano-cautery. "The left eye was secured, and the animal allowed to recover from stupor. At the end of half an hour it was evidently wide awake, but would not move unless touched. At this time it was removed from its cage and placed on the floor, whereupon it began to grope about in a sprawling manner, knocking its head against every obstacle. After some minutes of this behaviour it subsided, and refused to move. It made no sign of fear at threatening gestures, and did not wink at a thrust of the finger at its eye until the finger almost touched the conjunctiva, when the usual reflex closure occurred. Half an hour later the same tests were employed, with precisely the same indications of total loss of vision. At the end of still another half hour, while it was lying quietly in its cage, it was gently laid hold of without noise to attract its attention, whereupon it bounded away with an expression of fear and surprise, and ran full tilt against the leg of the table, where it remained groping and sprawling for a few minutes. It then started off, and this time ran against the wall, against which it sprawled helplessly. Similar things were repeated. It gave no sign of perception when it was cautiously approached without noise; but when a slight noise was made with the lips quite close to it, it darted off and came against the wall as before, where it lay down. Half an hour later, while it was resting quietly in a corner with its eyes open, the light of a lantern was flashed in its eyes, but it gave no sign. Creeping up to it cautiously without exciting its attention the observer made a slight whisper close to its face, whereupon it peered eagerly, but evidently remembering the results of running away it crouched down and would not move. Half an hour later, when it was quiet in its cage, it started suddenly on being touched, and ran its head into a corner, where it crouched.

"Next day, its left eye being still closed, it showed unmistakably the possession of vision with the right eye. It laid hold of things as usual, and ran about the laboratory in every direction, passing obstacles right and left with perfect precision, and ducking its head to pass underneath bars as it ran along the top of

26 See Experiments 3, 4, 5, 6, *Phil. Trans.*, vol. ii, 1884.

the waterpipes of the laboratory. No defect of vision, amblyopic or hemiopic, could be detected."[27]

In another animal, the left angular gyrus was cauterised up to the parieto-occipital fissure, the posterior part of the corpus callosum being also divided at the same time.[28]

"The left eye was securely closed, and the animals allowed to recover from its narcotic stupor. In half an hour it began to move about spontaneously, although rather unsteadily. An hour and a half after the operation it walked about the laboratory, knocking its head against legs of chairs and other obstacles in its path. When a piece of apple was held under its nose it grabbed it and ate. It continued to walk about here and there, every now and then coming to a dead halt full tilt against the wall. Three hours after the operation it again, in running about the laboratory, came full tilt with its snout against the wall, where it rested. While it was resting quietly we crept up to it; but the animal, though with eyes wide open and looking towards us, made no sign of perception. Threatening grimaces were likewise without effect; but on making a noise with our lips the animal seemed alarmed, peered forwards, and yet, though it came close to our faces, seemed to see nothing. It was tried to right and left in the same way, but there was no sign of vision to one side or the other. Next day, the left eye being still closed, the animal ran about in every direction, ducking under bars, passing objects right and left with the utmost precision, and never once knocking against anything one side or the other. Not the slightest impairment of vision could be detected, and it was able to pick up the minutest objects lying about its cage or thrown down near it."

It was first shown by Munk[29] that the permanent effect of complete unilateral extirpation of the visual sphere was not complete blindness of the opposite eye, but homonymous hemianopia, from paralysis of the corresponding sides of both retinæ. This effect he obtained by section in the line of the parieto-occipital fissure, and he localised the visual sphere exclusively in the occipital lobe, regarding the angular gyrus as the "sensory sphere" of the eye. Owing, however, to the fact, as he himself admits, that secondary inflammation and extension of the primary lesion generally, if not universally, followed his operative procedure, Munk's experiments cannot be relied upon when it is a question of the

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27 Experiment 5, *Phil. Trans.*, vol. ii, 1884.

28 Experiment 7, *op. cit.*

29 Ueber die Functionen der Grosshirnrinde, 1881.

exact delimitation of any given area. It is a reasonable supposition that Munk's operations for removal of the occipital lobe would be the cause of secondary implication of the angular gyrus or its connections. The question as to the exact delimitation of the visual sphere, whether it is confined only to the occipital lobe, according to Munk, or embraces also the angular gyrus, according to my view, and the respective relations of the angular gyrus and occipital lobe to the eyes has been the subject of investigation by numerous physiologists: Luciani and Tamburini,[30] Luciani,[31] Horsley and Schäfer,[32] Sanger-Brown and Schäfer,[33] Lannegrace,[34] Gilman Thompson and Sanger-Brown[35] and is still a matter on which opinions are far from being in accordance.

Luciani and Tamburini, and Luciani have arrived at the conclusion that the visual centres are not confined to the occipital lobes, but embrace also the angular gyri, though the former believed that the effects of unilateral destruction of the angular gyrus were hemiopic rather than amblyopic. The experiments of Horsley and Schäfer and of Sanger-Brown and Schäfer are of great value, as, owing to the use of antiseptic precautions, and the full details and figures which illustrate the experiments, their facts are available for all inquirers. Horsley and Schäfer record several experiments on the occipital lobe on one or both sides. The following experiment (24), which I give in their own words, is especially worthy of note. "The whole of the left occipital lobe was removed by an oblique incision along the parieto-occipital fissure. The piece removed included the extremity of the posterior cornu of the lateral ventricle, which was thus freely opened. No ill consequences resulted from this, however, and when on the fifth day the dressings were removed the wound was found to be completely healed. Result, no muscular paresis. The animal seems to have some disturbance of visual consciousness of the images of objects which fall upon the left side of the retinæ; for an object, such as a raisin, presented to it on the right side of the visual line, is either not noticed or its nature is not readily recog-

30 *Sui Centri Psico-Sensori Corticali*, 1879.

31 On the Sensorial Localisations in the Cortex Cerebri, *Brain*, July, 1884.

32 A Record of Experiments upon the Functions of the Cerebral Cortex, *Phil. Trans.*, vol. clxxix, 1888, B. 20.

33 Functions of the Occipital and Temporal Lobes of the Monkey's Brain, *Phil. Trans.*, vol. clxxix, 1888, B. 30.

34 Influence des Lésions Corticales sur la Vue, *Archives de Médecine Expérimentale*, 1889.

35 The Centre for Vision, *Researches of the Loomis Laboratory of the Medical Department of the University of the City of New York*, No. 1, 1890.

nised. This condition, which was very marked at first, gradually improved, until three months after the operation it could no longer be determined." Other portions of the hemisphere, as shown in the figure, were removed, but into the results of these it is not necessary for me here to enter. The appearance of the brain is given in their figures (24A and 24B), of which one represents the under surface, and, as the authors themselves say, "the representations are mainly of interest as showing the completeness of removal of the frontal and occipital lobes, and the limits of the lesion upon the under surface of the hemisphere."[36]

Several others are recorded in which the lesions, unilateral or bilateral, trenched on the parieto-occipital fissure and region of the angular gyrus, and in none of these was hemiopia or blindness absolute or permanent. In one case (Experiment 26), in which both occipital lobes (external and posterior surfaces and a part of the under surface) were removed, with an interval of fourteen days between the two operations, there seemed to remain a general impairment of visual perception, without, so far as could be made out, absolute blindness in any part of the field of vision, but of this they cannot speak with certainty. On the removal of the right angular gyrus complete left hemianopia was the result, which lasted, without any sign of improvement, until the animal's death, three months afterwards. Horsley and Schäfer's experiments, therefore, in which the lesions of the occipital lobes were perhaps more extensive than any of those described by Yeo and myself—my earlier experiments excepted—show that at most the hemiopic disturbances are transient, while, in the first case referred to, there appears to have been complete removal of the occipital lobe, and yet the hemiopia was not of permanent duration. Destruction of the angular gyrus, in combination with the occipital lobe, was the only lesion which caused a permanent result. Their conclusions, as stated in their own words, are as follows:—

"Our experiments upon the occipital region, although few in number, seem to link together the conclusions arrived at by Munk, and by Ferrier and Yeo as the results of their experiments. They indicate that both the occipital lobes and angular gyri are concerned with visual perceptions in such a manner that each occipital region is connected with the corresponding lateral half of

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[36] P. 35.

each retina, and that a part only of the cortex of the region in question is able to take on in great measure—how completely cannot be determined in animals—the functions of the whole. This is in conformity, also, with the results of Luciani. So far as the occipital lobe alone is concerned, our observations confirm the statement of Munk that the effect of this lesion is to produce a hemiopic disturbance of visual consciousness. But the imperfect vision which remains after removal of both occipital lobes (see Cases 25 and 26) suggests that the area which is concerned with visual consciousness is not confined to those lobes, as was inferred by Munk, but extends over into the angular gyrus, permanent hemiopia being produced by the subsequent removal of that convolution. It will, however, be necessary that further experiments should be undertaken, in order to determine more precisely, not only the extent, but also the relative importance of the anterior, posterior, and mesial portion of the visual area of the cortex."[37]

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[37] *Op. cit.*, p. 19.

LECTURE III.

LECTURE III.

Schäfer's further investigations, in conjunction with Sanger-Brown, led him to agree with Munk that complete unilateral extirpation of the occipital lobe alone caused persistent hemiopia, while bilateral extirpation caused total and enduring blindness. Admitting, however, that the lesions described by them were the cause of hemiopia or total blindness, it does not follow that these results are due to removal of the occipital lobe as such. Schäfer himself [1] admits that the visual area embraces not only the occipital lobe, but, perhaps also part, or the whole, of the angular gyrus. The relations of the different portions of the visual centres to the retinæ, founded on the phenomena of electrical irritation, as well as other facts, necessitate that the angular gyrus (its posterior limb at least, according to Schäfer) should be included in the visual area; more, therefore, than the occipital lobe proper. If total blindness, therefore, is caused by removal of the occipital lobes in the line of the parieto-occipital fissure, it is necessary to suppose that by this operation the medullary connections of the whole of the visual area become implicated. Schäfer [2] has himself suggested that fibres connected with the cortex of the adjoining parts of the brain, and especially of the angular gyrus, may be cut off along with the occipital lobe, and that this is the real explanation is supported by many considerations.[3]

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[1] Electrical Excitation of the Visual Area, *Brain*, April, 1888.

[2] *Brain*, vol. x, p. 372.

[3] This, however, does not fit conveniently into Schäfer's scheme, which is as follows:—1. The whole of the visual area of one hemisphere is connected with the corresponding lateral half of both retinæ. 2. The upper zone of the visual area of one hemisphere is connected with the upper half of both retinæ. 3. The lower zone of the visual area is connected with the lower part of the corresponding lateral half of both retinæ. 4. The intermediate zone of the visual area is connected with the middle part of the corresponding lateral half of both retinæ (*loc. cit.*, p. 5). The reactions would, however, be fully explained on the assumption that the angular gyrus has relations with the whole of the opposite eye.

Lesions of the occipito-temporal region alone are competent to produce hemiopia or complete blindness, according as the lesion is unilateral or bilateral, altogether apart from affection of the angular gyrus, or any other portion of the occipital lobe. I have myself recorded instances[4] in which lesions of the occipito-temporal region were followed by temporary hemiopia, and probably similar facts have led Luciani to extend the visual area into the temporal lobe. But, not only may temporary hemiopia occur, but the hemiopia so produced may be persistent.

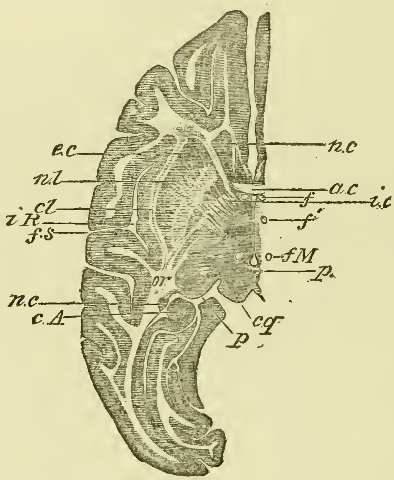

Fig. 12.—Horizontal section of left hemisphere of monkey—on a level with the anterior commissure (nat. size); *a.c.*, anterior commissure; *c.A.*, cornu Ammonis; *cl.*, claustrum; *c.q.*, corpora quadrigemina; *e.c.*, external capsule; *i.c.*, internal capsule; *i.R.*, island of Reil; *f.*, anterior or descending (Meynert) pillar of fornix; *f'.*, ascending fibres or Vicq d'Azyr's bundle; *f.M.*, Meynert's fasciculus; *f.S.*, fissure of Sylvius; *n.c.*, nucleus caudatus; *n.l.*, nucleus lenticularis; *o.r.*, optic radiations (Gratiolet); *P.*, pulvinar; *p.*, posterior commissure.

Here is an illustration[5] of the brain in one of Brown and Schäfer's experiments. The operation consisted in removal of the right temporal lobe. Posteriorly, the lesion extended partly over the under surface of the occipital lobe. With the exception of this lesion of the occipital lobe, all the rest of the visual sphere was intact, yet this animal was completely hemiopic. The inference is that the lesion severed the whole of the optic radiations, for,

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[4] *Phil. Trans.*, vol. ii, 1884, Experiments 27 and 28.
[5] Figs. 4a, 4b, *Phil. Trans.*, 1888, B. 30, plate 49.

otherwise, it should, on Schäfer's hypothesis, have caused blindness only of the lower portions of the retinæ.

It appears, therefore, that the incision for the removal of the occipital lobe carried along the line of the external parieto-occipital fissure is calculated to sever the whole of the optic radiations of the occipito-angular region, which emerge from the primary optic nuclei about this level. (See Fig. 12). In support of this I quote the following experiment: I exposed the lower extremity of the left external parieto-occipital fissure, and, in-

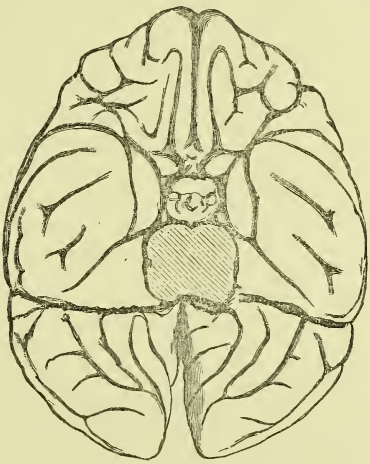

Fig. 13.

serting a director at this spot between the lower surface of the occipital lobe and and the tentorium, passed a stylet bent at an oblique angle along the groove in such a manner as to make a transverse incision a few millimètres in depth across the occipito-temporal region. The result of this was right hemiopia, which, however, speedily passed off, so that it was no longer clearly perceptible on the third day. A fortnight afterwards the right occipito-temporal region was similarly operated upon, the incision this time being made just anterior to the lower extremity of the parieto-occipital fissure. The animal died a month after the first operation. During the whole time it survived it remained absolutely hemiopic towards the left in every part of the visual field. It was found after death (see Fig. 13) that the incision on the left side was shallow and not continuous, being interrupted in the region of the lingual lobule. On the right side the incision extended across the whole occipito-temporal region, and penetrated several millimètres into the substance of the brain, dividing the medullary fibres emerging from the region of the primary optic centres.

Brown and Thompson[6] believe that removal of the occipital lobe on one side causes hemiopia to the opposite side, altogether apart from lesion of the angular gyrus, which they entirely exclude from the visual sphere. They give particulars of a monkey, in which, after removal of the left occipital lobe, right hemiopia resulted, together with right hemianæsthesia, which was still observable on the twenty-sixth day after the operation. One hundred days after the first operation the right occipital lobe was similarly removed. This was followed by complete blindness, but they state that after three weeks the animal recovered vision to some extent towards the left. They assume—but furnish no evidence of the fact—that probably a few occipital fibres had escaped injury during the second operation. The animal died of phthisis on the 231st day. On examination it was found that the entire occipital lobe behind the angular gyrus upon each side had been removed, leaving a clean-cut surface. For some distance around this surface the pia mater was firmly adherent to the convolutions beneath, but it was stated not to have been thickened. It is certain, however, that their first lesion must have extended beyond the occipital lobe, owing to the hemianæsthesia, which does not occur when the lesions are restricted to the occipital lobe itself; and that the removal of the occipital lobes, as such, which they appear to have found equally complete on both sides, did not cause total loss of vision, is shown by the fact, which they themselves record, that the animal was still able to see, even if imperfectly, towards one side. In a second experiment they found that destruction of the left angular gyrus caused no result beyond hemianæsthesia on the right side, together with some paralysis of the right arm (!). On the ninetieth day a second operation was performed, consisting in excision of the whole of the right occipital lobe. This was followed by left hemiopia, which still persisted when the paper was written, seventeen months after the operation. These are the only experiments on monkeys which these authors have recorded. Lannegrace,[7] on the other hand, who has performed numerous experiments on the occipital lobes and angular gyri of monkeys, states, in accordance with my own and Yeo's results, that destruction of the occipital lobe causes no

[6] *Op. cit.* [7] *Op. cit.*

appreciable impairment of vision, whereas destruction of the angular gyrus produces crossed amblyopia of a temporary character. He reports two cases of successive lesion of the angular gyri. In the one the first lesion induced crossed amblyopia, which lasted four days. The second lesion, however, produced no appreciable alteration. In the other the first lesion again caused crossed amblyopia, which disappeared in two days, while the second gave rise to lasting amblyopia. These results, which are similar to those obtained by Yeo and myself, depend, no doubt, on the degree of completeness of extirpation of the gyri.

I have already mentioned that my earlier experiments, as well as those made by Professor Yeo, show that unilateral destructive lesion of this gyrus caused temporary blindness of the opposite eye, and that bilateral destruction caused for the time complete blindness in both eyes. Though these results have been much questioned, I must insist on their accuracy. I have corroborated the occurrence of apparently complete blindness of the opposite eye, on destruction of the left angular gyrus in an animal which I lately made the subject of experiment. In this animal I had previously enucleated the left eye, so as to exclude all complications from this side. After removal of the left angular gyrus, however, the animal, though otherwise well and in complete possession of all its senses and motor powers, was evidently absolutely blind. It responded to no test of vision; would not budge from the spot, but when urged to move sprawled blindly and helplessly. This condition lasted for several hours, during which it was under observation. Next day there were indications of vision, but the animal had become so prostrated, the weather being intensely cold, that it died before any further exact observations were possible. That lesions of the angular gyrus may cause implication of the optic radiations is possible, but this result is neither necessary, nor would it account for complete loss of vision in the opposite eye. The bilateral relations of the angular gyrus account for the transient nature of the amblyopia which results from unilateral extirpation, and, as in few of my experiments was the destruction of this gyrus complete on one side or the other, it occasionally happened that removal of the other gyrus some time subsequently did not seem to impair vision either on one side or the other. When, however, the angular gyri are completely destroyed on both sides, the animal, though for the first three or four days absolutely blind, does not remain so permanently, but it never regains normal vision. This also has been confirmed by the researches of Lannegrace. Apart from the affection of vision, destruction of the angular gyrus causes no other symptoms, either motor or sensory; there is no ptosis or paralysis of the ocular muscles, and the sensibility of the conjunctiva is absolutely unimpaired.

These results, confirmed by the researches of Horsley and Schäfer, contradict the statement of Munk that the angular gyrus is the sensory sphere of the eyeball; and it will be found, on examination of Munk's own data, that the phenomena on which he relies as indicating loss of the sensibility of the eye are in reality due to loss of vision. Thus he says that after destruction of the left angular gyrus approximation of the finger to the left eye invariably caused winking, whereas the same threat against the right eye caused winking only when the eyelids were actually touched. This appears to be a proof of the sensibility of the eye, and the non-perception of threatened danger at a distance. The absence of winking at threatened danger he admits to be characteristic also of blindness, but he argues that, inasmuch as the animal could not be blind, presumably because the occipital lobe was intact, therefore, the non-occurrence of winking could only be due to the inability of the cortex to act on the sphincter palpebrarum! Again, he says, that when the angular gyrus has been destroyed on one side, and the eye on that side closed, the animal often fails to seize things offered it, or thrown down before it, especially when the objects are small. This I consider a clear indication of amblyopia. And he also states that after bilateral extirpation of the angular gyrus of monkeys, "after incomplete restitution"—a phrase, however, which is not very intelligible—are unable like normal monkeys to take things offered them delicately with the fingers, but make grabs at them with the whole hand. This is only a further illustration of the same imperfection of vision which I have described—namely, want of precision in prehension, and a continual tendency to place the hand over or short of the object aimed at, instead of on it at once.

Schäfer also[8] records the symptoms in a monkey in which he destroyed both angular gyri. For the first few days the animal appeared totally blind, but vision gradually returned, and before long was quite good for distant objects. The animal could apparently see small objects, such as a raisin, at a distance, but on running up to it seemed to have some difficulty in finding it.

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[8] *Brain*, July, 1888, p. 159.

Schäfer is of opinion that this latter fact is due to absence of vision in the antero-superior and lateral portions of the retinæ. I have lately carefully investigated the condition of vision in a monkey in which I had completely destroyed both angular gyri. There was no ptosis, the ocular movements were normal, the conjunctival reflexes unimpaired, sensibility was intact everywhere, and the motor powers were perfect, but, for four days at least, the animal was evidently absolutely blind. When urged to move it ran against every obstacle in its path, paid no attention to threats, could not find its food, except by groping, and appeared insensible to light flashed in its eyes. On the fifth day there were evidences of returning vision. It did not now knock its head against obstacles; would not walk over the edge of the table; showed signs of perception of light flashed in its eyes, and occasionally seemed to wince when threatened. Vision gradually improved, but continued very imperfect, especially for minute objects, which it rarely, if ever, seized quite precisely; groping at them with the whole hand, and reaching short, or over, or to the side. It appeared to see objects held above, below, and to either side much better than those held in front of its eyes. Six weeks after the operation my colleague, Professor McHardy, examined the animal, which was very docile, with me, testing every portion of the visual field by pieces of apple suspended by a delicate thread. It was concluded that vision was better in every part of the periphery than in the centre. Objects held directly before the eyes and at a little distance were apparently not clearly seen, and never laid hold of with precision. The condition remained unchanged for three months after the operation, similar tests being from time to time applied, and with the same result. I noted also that the animal, when examining any object, always held it at full arm's length from its eyes. The phenomena observable in this animal were such as would be best explained by impairment or loss of central vision; for it is well known that when central vision is lost or impaired in man, objects are better seen at a distance than close at hand, and less distinctly when the eyes are immediately converged on them. This is practically the condition seen in this animal. The loss of central vision would thus account for the fact, noted by Schäfer in his animal, that objects were better seen at a distance than near at hand; and that Munk's animal could never place its fingers precisely on any small object held directly in front of its eyes. There was certainly no indication, but the reverse, that the upper portions of the retinæ were less sensitive than the lateral and lower portions. It appears to me, therefore, that the symptoms resulting from bilateral destruction of the angular gyrus, described by myself, Munk, and Schäfer, are best explained on the supposition that the angular gyri are more particularly related to the area of distinct vision, and, accordingly, with the maculæ luteæ. The facts of disease in man render it necessary to assume that the region of the yellow spot is represented in each hemisphere, though more in that on the opposite than on the same side, and the probability is that the area of clear vision is represented mainly in the angular gyrus of the opposite hemisphere.

The retinal relations of the visual centres are not capable of being explained by a simple division of the retinal fields into co-related halves projected on the corresponding side of each hemisphere. For unilateral lesion of the angular gyrus produces a temporary blindness or amblyopia of the opposite eye; while bilateral destruction induces an enduring impairment of visual acuity in both eyes.[9] The results of my experiments seem to show that the angular gyrus has relations with both eyes. The crossed action, however, is the only one which is clearly demonstrable in the lower animals, but this does not exclude the possibility of some impairment of vision on the same side, not perceptible by tests applicable to them. It is certain that in man affections of the visual centres occasionally produce crossed amblyopia, and not homonymous hemiopia. Not only is this characteristic of the visual disturbances seen in hysterical hemianæsthesia, the pathology of which is obscure, but it has been noticed also in cases of organic disease. Usually, along with the blindness, or great impairment of vision in the opposite eye, there has been some degree of contraction of the visual field of the eye on the same side. I have myself reported several such cases,[10] and Gowers[11] has also seen similar instances. A well-observed case of this nature has been recorded by Sharkey.[12] *Post-mortem* examination revealed softening and absorption of a considerable area of the opposite hemisphere, including the angular gyrus. The occipital lobe was intact, and in nowise reduced in size as compared with the other.

[9] This accords with Gowers's hypothesis that "on the outer surface, in front of the occipital lobe, there is a higher visual centre in which the half fields are combined, and the whole opposite field is represented." (*Diseases of Nervous System*, vol. ii, p. 19.)

[10] Cerebral Amblyopia and Hemiopia, *Brain*, vol. iii, p. 456.

[11] *Diseases of the Nervous System*, p. 19.

[12] *Medico-Chirurgical Transactions*, vol. lxvii, 1884.

A distinguishing test between tract and central hemiopia has been suggested by Wilbrand,[13] and advocated by Wernicke and Seguin, which consists in determining whether a pencil of light thrown on the blind side of the retinæ induces contraction of the pupil or not. As the optic tract is the path of the fibres which excite pupillary contraction through the oculo-motor centres, as well as those which excite visual sensations in the cortex, lesion of the optic tract will cause not only hemiopia, but also paralysis of the reflex reaction of the pupils to light; whereas, lesion of the cortical centres will cause hemiopia, but leave intact the pupillary reaction. This test, however, requires great care in its application, as it is difficult to restrict the rays of light entirely to the blind side. In a case recently under my care at King's College Hospital,[14] in which the dividing line passed through the fixation point, and which was carefully investigated in this relation by Professor McHardy and myself, the pupillary reaction was not obtained, as a rule, when the pencil of light was thrown on the right side of the retinæ; whereas it occurred readily when the light was thrown on the left half of each retina. These facts, therefore, would corroborate the hypothesis that this was a case of tract hemiopia.

I have recently verified the hemiopic pupillary reaction in two monkeys in which I accidentally severed the optic tract in establishing lesions of the temporal lobe. The result in both cases was absolute hemiopia to the opposite side. In both cases the left optic tract was divided, and in both, along with right hemiopia, there was absence of reaction of the pupil when a fine pencil of electric light was thrown on the left half of each retina; whereas, active reaction took place when the light was thrown on the right half. Both in the monkey, and in several cases of hemiopia in man depending on lesions of the hemisphere, I have found that the pupillary reaction is equally well marked whichever side of the retina is illuminated. There can be no question that in man and monkeys there is decussation of the optic tracts in the

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[13] *Op. cit.*

[14] The patient was a man, aged 39. Two years before he had contracted syphilis, and at the time of his admission was suffering from a large tertiary ulcer on the soft palate. He had twitching of the right side of the face, together with weakness and numbness of the left side. The left hand grasp was weak, and there was loss of dorsal flexion of the left foot. The tongue deviated to the right on protrusion. He was found to be absolutely hemiopic towards the left side, and a careful perimetric examination by Professor McHardy demonstrated that the dividing line passed exactly through the fixation point.

chiasma. Michel, in his comparatively recent monograph,[15] still maintains the contrary, on the basis of microscopical investigation; but his results have been attributed by Singer and Münzer[16] to imperfect methods of examination.

In reference to the pathology of crossed amblyopia from lesion of the angular gyrus in the monkey, as well as of similar cases of disease in man, I may here allude to the hypothesis advanced by Lannegrace. Lannegrace regards the eyeball as innervated by two sets of fibres—sensorial, or optical proper, and sensory, on which the proper nutrition of the eyeball depends. The sensorial, or optical, decussate in the chiasma, and are distributed to the occipital lobe; while the sensory decussate in the pons, and, applying themselves to the posterior fibres of the internal capsule, are distributed mainly to the angular gyrus. Lesions of the sensory fibres produce amblyopia and sensory disturbances in the eyeball. A similar result follows lesion of the angular gyrus, and is essentially dependent upon changes which are induced in the nutrition of the eye. This hypothesis would require that in all cases of amblyopia from cerebral lesion there should be impairment of sensation in the eyeball. But this is certainly not the case, for, though in hysterical amblyopia there is affection of common sensation as well as of vision, it is not so in the amblyopia following destruction of the angular gyrus. Though affections of the fifth nerve, which cause loss or impairment of sensation of the eyeball, frequently also lead to trophic disorders of the eye, yet this is not necessarily so; and, even when the eyeball is absolutely anæsthetic, provided that no trophic disturbances have occurred, vision is not in the least impaired. In proof of this I would refer to cases (Cases I and III) reported by Hutchinson in the *Ophthalmic Hospital Reports*, vol. iv, 1863-65. Nor does complete anæsthesia of the eyeball induced by cocaine impair the visual acuteness of the eye.

These appear to me to be fatal objections to the hypothesis advanced by Lannegrace, and I contend that the only hypothesis which seems to harmonise with all the facts is, that the angular gyri are more particularly the centres for clear vision, each mainly for the eye of the opposite side. Whether the other portions of the retinæ, upper, lower, outer, and inner, are specially represented in corresponding regions of the occipital lobe, according to the hypotheses of Munk and Schäfer, cannot be said to have

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15 *Ueber Sehnerven-Degeneration und Kreuzung*, 1887.

16 *Beiträge zur Kenntniss Sehnervenkreuzung*, 1889.

as yet been established; for, even after the most extensive destruction of the occipital lobes, no portions of the retinæ appear to be absolutely blind; hence, even if we admit that the effects of irritation probably indicate a special relation of the different portions of the visual field to certain portions of the occipital cortex, the relation, so far as we may judge by the facts of disease or experimental lesion, does not seem to be an exclusive one.

It is true that in man we sometimes find, besides general hemiopic deficiency, partial, quadrant or sector-like, defects in the upper or lower halves of the visual field. These appear, however, to be merely incomplete hemiopia, and occasionally, as in the case which I show you, an islet of subnormal visual acuity may be seen in the defective half. The pathology of these sector-like defects is a matter of conjecture. They have not been conclusively brought in relation with lesions of any particular portion of the cortex, and the probability is that they are dependent rather upon partial lesions of the optic radiations than of the cortical centres themselves. This was without doubt the pathology in the case which I have alluded to, for the defect occurred in a patient who had a sudden attack of hemiplegia accompanied by hemianæsthesia and some affection of speech.

It is doubtful whether there are on record any cases of strictly cortical lesions of the occipital lobe proper, accompanied by hemiopia, apart from direct or indirect implication of the optic radiations. In most of the cases of hemiopia which have been examined after death, in which the optic tracts, optic thalami, or corpora geniculata have not been obviously diseased, the lesions have been found in the medullary fibres of the posterior region, vaguely or inaccurately called the occipital lobe; or, if the cortex has been mainly affected, the lesions have been multiple and diffuse, and not confined to the occipital region. And in addition to hemiopia, there have been hemiplegia, hemianæsthesia, aphasia, or other symptoms of implication of the cerebral tracts and centres beyond those of the occipital region.

Under my direction, my friend and pupil, Dr. Ewens, has collected and analysed the majority, if not all, of the recorded cases of hemiopia (with necropsies) depending on cerebral lesions which have not obviously been of such a character as to cause indirect and indefinite implication of other regions. Of 41 cases of hemiopia, 15 were from disease of the occipito-angular region, 2 were cases of disease of the angular and supramarginal gyri only, 15 were described as being from disease of the occipital lobe alone. Of these 15, there were only 2 (Hun's case[17] and Doyne's case[18]) in which there was not either a tumour, cyst, abscess, or scftening of the medullary substance of the occipital region, or another lesion affecting the optic thalamus; and in 1 of these cases (Doyne's), the position of the lesion was not accurately described.

In the other cases the lesions were of a diffuse character, 6 being from lesion of the occipito-temporal region, and 3 from lesion of the occipital, temporal, and parietal lobes simultaneously, the angular gyrus being implicated in all.

From the comparative frequency with which hemiopia has been found associated with lesions of the cuneus and its neighbourhood Seguin[19] and Nothnagel[20] are of opinion that this portion of the occipital lobe has a special relation to visual perception; while Wilbrand believes that the visual centre is more especially in the apex of the occipital lobe. These hypotheses are not supported by experimental research. The probability is that any apparent relation between lesions of the cuneus and the occurrence of hemiopia, is due to the special proclivity of this region to affection by morbid vascular conditions, and to coincident implication of the optic radiations of the occipito-temporal region. In Seguin's own case,[21] on which he relies in support of his hypothesis, not only was the cuneus implicated, but also the fourth and fifth temporal gyri and a part of the gyrus hippocampi.[22] Cases have also been recorded in which, not only unilateral, but bilateral lesions have been found in the occipital lobes without any affection of vision whatever.

Irritative lesions of the angular gyrus occasionally give rise to optical illusions, or flashes of light, followed by temporary amblyopia, as recorded by Hughes Bennett[23]; while destructive lesions of the angular gyrus, more particularly in the left hemi-

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17 *Amer. Journ. Med. Sci.*, 1887, Case i.

18 Ophthal. Soc., Lond., November 14th, 1889.

19 *The Journal of Nervous and Mental Diseases*, vol. xiii, January, 1886.

20 *Neurolog. Centralblatt*, 1887, p. 213.

21 *Op. cit.*

22 Since this was written a case has been put on record by Delépine (*Trans. Path. Soc. Lond.*, May 20th, 1890) in which right hemiopia was apparently associated with softening of the left cuneus. In this case, however, there was general arterial degeneration, and there were many circumscribed patches of softening in various parts of the brain. In particular there was a small area which had destroyed the greater part of the middle occipital convolution. This case is, therefore, too complex to allow of exact conclusions as to the connection between the hemiopia and the lesion of the cuneus in particular.

23 Excessive Sensory Cortical Discharges and their Effects, *Lancet*, March 30th and April 6th, 1889.

sphere, are generally associated with the special form of sensory aphasia termed "word-blindness" (Kussmaul). Word-blindness is not necessarily accompanied by any noteworthy affection of visual sensation, though in some cases, where the lesion of the occipito-angular region is more extensive, there may be a greater or less degree of right hemiopia.

On the other hand, right hemiopia, pure and simple, is not necessarily associated with any defects in visual ideation. This would be an argument against its cortical nature. The fact that visual ideation, more particularly in reference to the association of written symbols with their meanings, is apt to suffer more readily than simple perception, appears to me to illustrate the laws of the evolution and dissolution of the nerve centres, which have been so ably expounded by Hughlings Jackson in his Croonian Lectures delivered here a few years ago (1884). As evolution is from the most simple and most stable up to the most complex and least stable, so destructive processes annihilate first of all the higher, and last of all the lower functional manifestations. The functions of the visual centres in respect to mere visual sensation, or simple presentation, are much more stably organised than those which imply visual ideation or re-presentation, and in particular such highly specialised and complex processes as are involved in the association between visual symbols and things signified. Hence, a lesion of the area of clearest vision may paralyse visual re-presentation, while the simpler function of visual presentation may not be appreciably impaired. In order that this also should be entirely abolished it is necessary that every trace of the given centre should be extirpated. In other words, re-presentative blindness will occur sooner than presentative blindness, and the former more readily in its most specialised modes of manifestation.

In regard to the visual centres of the lower vertebrates, I cannot quote many observations or experiments of my own. The visual centres of dogs have been the chief subject of physiological investigation. Hitzig[24] first noted the occurrence of blindness in the opposite eye from destruction of the occipital region in dogs; and in 1881 Goltz described an affection of vision resulting from destructive lesions of the opposite cerebral hemisphere, which, however, he did not specially associate with lesions of the occipital lobe, though he has more recently admitted this relationship. The affection in question

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[24] *Centralblatt f. d. med. Wissenschaften*, 1874.

was, in his opinion, not complete blindness, but an inability on the part of the animal to understand or interpret what it saw. To this condition he gave the name *Hirnsehschwäche*, or cerebral amblyopia. It was entirely crossed, and affected only the eye on the side opposite the lesion. Munk, in his first experiments, arrived at essentially the same conclusion; namely, that the affection of vision resulting from lesion at the point A, Fig. 14, occurred only in the opposite eye. Dalton [25] also found that the opposite eye was rendered blind, and to all appearance permanently so, when the cortex was destroyed in the region of the

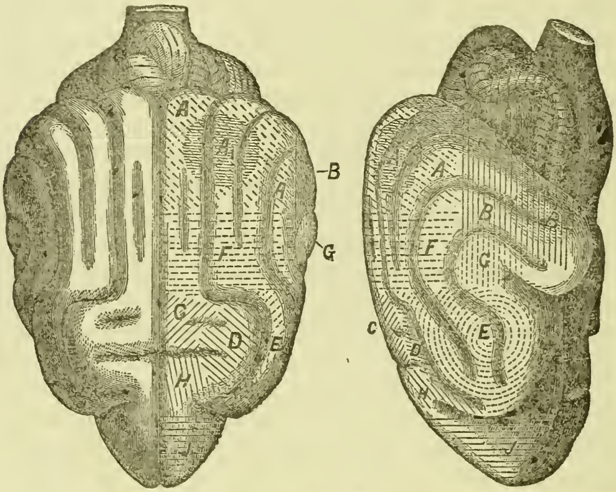

Fig. 14.—Cortical centres of the dog, after Munk. *A*, Visual area; *B*, auditory area; *C* to *J*, tactile sensory area (*Fühlsphäre*); *D*, fore-limb region; *C*, hind-limb region; *E*, head region; *F*, eye region; *G*, ear region; *H*, neck region; *J*, trunk region.

posterior division of the second external convolution, which he terms the angular convolution. Luciani and Tamburini, on the other hand, found that destruction of the second external convolution, more particularly of its median or parietal portion, caused blindness of the opposite eye, and also some degree of amblyopia of the eye on the same side. The further experiments of Munk, however, as well as those of Loeb [26] and of Goltz,[27] and also the later experiments of Luciani,[28] appeared to show that though in

[25] Centres of Vision in the Cerebral Hemispheres, *Med. Rec.*, 1881.
[26] *Pflüger's Archiv*, Bd. 4., 1884.
[27] *Ibid.*, p. 450.
[28] Sensorial Localisations in the Cortex Cerebri, *Brain*, vol. 7, 1885, p. 145.

dogs the visual area is mainly in relation with the opposite eye, it is also in relation with the outer quadrant of the eye on the same side. Hence, destruction of the visual centre in the one hemisphere paralyses the inner three-fourths of the opposite retina, and the outer fourth of the retina on the same side. The condition, therefore—at least the enduring one—is that of homonymous hemiopia towards the opposite side: the defect in the eye opposite greatly exceeding that in the eye on the same side. But the facts recorded by Luciani and Tamburini indicate that, for a short time at least, after the destruction of the middle portion of the second external convolution there is blindness in the opposite eye. And Goltz [29] remarks that he does not think that his former conclusions were due to defective observation, but that there was probably some variation in his operative procedure. It is, however, likely that we have here the same relations as exist in monkeys, and that, for the time at least, after complete extirpation of the visual sphere, there is total blindness in the opposite eye. This is confirmed by the experiments of Bechterew, recently published.[30] Bechterew finds that in dogs and cats there are two regions in the cortex related to vision; the one in the occipito-parietal region, in relation with the corresponding halves of both retinæ; the other, more especially in the parietal region, in relation with the opposite eye alone. Lesion of the former causes homonymous hemiopia; lesion of the latter, generally, possible only in association with the former, causes, along with hemiopia, amblyopia of the opposite eye by paralysing the centre of clear vision. This combined affection usually after a time gives place to homonymous hemiopia; or, on the contrary, the hemiopia disappears and the crossed amblyopia remains. Bechterew's conclusions may serve to explain, among others, the results arrived at by Gilman-Thompson and Sanger-Brown,[31] which appear to be entirely at variance with those of Munk, Goltz, and most other physiologists. For they find that lesions, of sufficient size and depth, in the posterior part of the occipital region in cats and dogs, invariably cause blindness of the opposite eye, with no impairment of vision in the eye of the same side. These authors, however, seem to think that the extent of the visual sphere is a matter more of cubical capacity than accurate anatomical localisation; for they say that in order that the blindness should be

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29 *Op. cit.*, p. 48.
30 Abstract in *Neurolog. Centralblatt*, April, 1890.
31 *Researches of the Loomis Laboratory*, 1890.

permanent, between 2.5 and 3 cubic centimètres of brain tissue should be removed in cats; and between 4.5 and 6 cubic centimètres in dogs. To render the blindness permanent, the incision must be at least 0.5 centimètre deep, and 2 centimètres in diameter, in cats; and 1 centimètre deep, and 3 centimètres in diametre, in dogs; and it must involve at least two convolutions. Smaller lesions produce complete blindness of the opposite eye, lasting from a day or two to six weeks. They conclude from their experiments that in cats and dogs there is complete decussation of the optic nerves in the chiasma. This is, however, opposed by the researches of von Gudden,[32] which show that in dogs and cats there is partial decussation of the optic tracts; and Nicati[33] found, experimentally, that division of the chiasma in the antero-posterior, or sagittal diameter, did not cause complete loss of vision in either eye. The recent researches of Singer and Münzer, previously alluded to, indicate that there is only partial decussation in the chiasma of the cat, dog, and also in the rabbit.

The exact limits of the visual sphere in dogs are still the subject of some differences of opinion, but all the experiments agree in including in this area the posterior half of the second external convolution. This is the convolution which in its electrical reactions corresponds with the angular gyrus and occipital lobe in monkeys. The visual area, as defined by Munk, is represented in the accompanying figure (Fig. 15). Point A, situated chiefly in the posterior division of the second external convolution, he regards as the centre of clear vision (macula lutea) of the opposite eye. The mesial portion of the visual sphere adjoining the falx he regards as the centre for the inner half, the anterior portion for the upper half and the posterior portion for the lower half of the opposite retina. The lateral portion he regards as the centre for the outer quadrant of the eye on the same side. Destruction of each portion he states induces blindness in the respective region of the eye on the opposite or same side accordingly, and it is only by abnormal fixation of the eyes, or by practice, that the animal is able to overcome the defects so induced.

Munk describes, as the effects of extirpation of a circular area of the cortex in region A, measuring about 15 millimètres in diameter and 2 millimètres in thickness, a condition of vision, or visual perception, similar to that already defined by Goltz. The animal is not blind, inasmuch as it is able to avoid obstacles, but it appears

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[32] *Archives f. Ophthalmologie*, 1874, Band 20.

[33] *Archives de Physiologie*, 2nd Series, Tome 5, 1878.

to have lost all visual ideation. To this affection he gives the name *Seelenblindheit* or "psychical blindness," in contradistinction to *Rindenblindheit* or "cortical blindness," which implies total loss of vision presentative, as well as re-presentative. In ex-

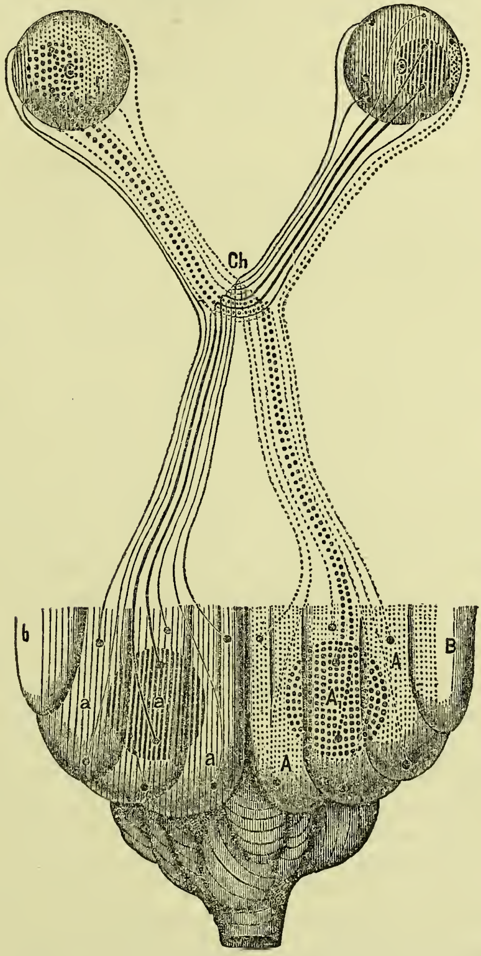

Fig. 15.—Relations of the eyes to the visual area in the dog (after Munk).

planation of this condition he propounds what appears to me a somewhat crude hypothesis, viz., that extirpation of the region in question has removed all the visual pictures which are stored up in and around the spot, and that it is only by a process of education that the animal again acquires a new stock of pictures which are deposited in the undestroyed portion of the visual sphere. Some pictures, however, apparently less fragile than the rest, may escape the general destruction occasioned by this iconoclastic lesion. In one case it is the picture of the dish out of which the animal has been accustomed to drink; in another it is the sign to "give the paw," which the animal has been accustomed to obey. Goltz has criticised this hypothesis in the following amusing terms:—

"A considerable portion of the cortex of the occipital lobe is described as the visual area by Munk. By far the larger portion of this area, however, is, according to him, pure luxus. The memorial pictures (*Erinnerungsbilder*) of the visual perceptions are huddled together like sheep in a storm, in a narrow spot which occupies only about two-sevenths of the whole visual area. When this small spot, which corresponds to the macula lutea of the human retina, is destroyed on both sides the animal is at first blind, and only gradually learns to see, like a puppy, with the aid of the rest of its visual sphere. Five-sevenths of the visual sphere —a large portion of the cortex—appears retained in order that a dog which falls into the hands of the physiologist should again learn to see, when its accumulated visual pictures are cut out. All dogs which escape this fate—and these, since the creation of the dog, must be very many—carry during their life five-sevenths of their visual sphere as an uncultivated fallow field. A wonderful thing in hypotheses!"[34]

Even if it were the case that the different portions of the retina are represented in the indicated regions of the visual area, it is improbable that these could be determined with any degree of certainty except by exact perimetric investigation, which is naturally impossible in the lower animals. The difficulties of deciding questions of this kind in the lower animals are illustrated by Munk's account of his experiences with rabbits.[35] "I had at least believed that I could determine with which eye the rabbit saw better, and with which it saw worse. In this, however, I have been mistaken, because it occasionally happened to me that where from tests I had thought I had made out that the greater imperfection of vision existed in the left eye, *post-mortem* examination revealed the fact that the left tract and the right optic nerve were more atrophied than the right tract and the left optic nerve."

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[34] *Op. cit.*, p. 175.

[35] *Sitzungsberichte Akad. d. Wissensch. zu Berlin*, vol. xxxi, June 20th, 1889, p. 631.

Loeb, after a series of carefully devised experiments, concludes that there is no foundation for the views of Munk that particular segments of the retinæ are in special relation to definite regions of the visual area. When defect of vision occurs from lesion of the posterior lobe, it is always of the same hemiopic or hemiamblyopic character, whatever portion of the visual sphere be injured. The lateral portion of this sphere is not in special relation with the outer quadrant of the eye on the same side, nor is any portion more in relation with one part of the opposite retina than another. In particular, central vision is precisely that which is least affected in all cases, whether of unilateral or bilateral lesion of the visual zone. There is never any eccentric or abnormal fixation of the eyeballs when the special regions indicated by Munk are destroyed, such as would necessarily result if the corresponding portions were paralysed, nor is the recovery of vision, after partial lesions of the visual area due to practice, or to the acquisition of new visual experience, inasmuch as recovery takes place when the animal is kept absolutely in the dark, and thus prevented from exercising its visual faculties.

In rabbits the visual centre would, according to the homology of the electrical reactions, occupy the parieto-occipital region of the hemisphere. The exact limits of the visual zone of these animals do not appear to have been accurately determined by any observer, though certain experiments of Moeli[36] point to lesions of the region indicated as causing, at least, temporary blindness of the opposite eye. It has been supposed that in this animal there is complete decussation of the optic tracts in the chiasma, inasmuch as the experiments of Brown-Séquard have shown that sagittal division of the chiasma causes complete loss of vision of both eyes. The total decussation in the chiasma of the rabbit was also supported by the earlier researches of von Gudden, who found that after enucleation of one eyeball the opposite optic tract only became atrophied.[37] But, in his later researches, he concluded that a small fascicle of uncrossed, or direct, fibres exist also in the optic tract of this animal, similar to that seen in higher vertebrates. Singer and Münzer are also of opinion that there is only partial decussation in the chiasma of the rabbit, but the uncrossed tract does not run as a separate bundle, but as fibres more or less diffused throughout the optic tract. In the mouse and guinea-

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[36] *Archives de Physiologie*, 1871-72: Sur les Communications de la Rétine avec l'Encéphale.

[37] *Archiv f. Ophthalmologie*, Bd. 20, 1874.

pig, however, the decussation is a complete one. The partial decussation of the optic tracts in the chiasma would favour the opinion that, in the rabbit also, both eyes are more or less in relation with each visual zone; and certain experiments of Munk would seem to favour this notion. The point, however, is one which requires further investigation.

In pigeons, and in birds in general, the region which in its electrical reactions is homologous with the visual centre of the higher animals occupies the parieto-posterior aspect of the hemisphere, where it forms a thin lamina over the corpus striatum. McKendrick[38] found that destruction of this region caused blindness in the opposite eye; whereas removal of the anterior part of the hemisphere had no effect on vision, nor removal of the posterior extremity of the hemisphere. Similar results have been obtained by Jastrowitz[39] and Musehold.[40] Blaschko, however, found that vision did not seem entirely abolished in the opposite eye by destruction of the cortex in the region indicated; and Munk came to the conclusion that though vision at first seems entirely abolished in the opposite eye, yet, after a time, it is regained in the extreme outer or lateral portion of the retina.

It is usually stated that in pigeons a complete decussation of the optic tracts occur in the chiasma, but von Gudden expresses some doubts on this point. Singer and Münzer, however, believe that in the pigeon a total decussation occurs. Munk quotes, in favour of his conclusions, certain observations by Müller to the effect that in the retina of the pigeon there is, besides the usual fovea centralis, another fovea, situated nearer the temporal region of the retina. The outer foveæ would subserve binocular, and the central foveæ monocular vision. These statements have been supported by the ophthalmoscopic investigations of Hirschberg.

It has seemed to me that if any bird can possess binocular vision it should be the owl, whose eyes are placed almost in the same plane. To decide this question I recently completely extirpated the right hemisphere of an owl. The right eye was then securely closed. The owl reacts very readily to visual tests, and is keenly alive to every movement coming within its field of vision. This bird, however, for ten days at least, remained perfectly indifferent to the electric light flashed in its eye, to all kinds of threats, and when urged to move flew blindly against

[38] *Trans. Roy. Soc. of Edinburgh*, January, 1873.

[39] *Archiv f. Psychiatrie*, Bd. vi, 1876.

[40] *Experimentelle Untersuchungen über das Sehcentrum bei Tauben. Diss inaug.* Berlin, 1878.

every obstacle in its course. At the end of this time there were indications of vision, which were found, however, to depend on the partial unclosure of the right eye. In order to ascertain if the visual centre of the left hemisphere was undamaged, the right eye was completely freed from its closure. This had the effect of restoring the animal's sight, so far as the right eye was concerned, though no indications of vision could be made out in the left eye. The bird was able to pursue and ultimately catch a mouse introduced into its cage, though the mouse frequently escaped for the time by getting to the owl's left. The right eye was then removed. It then speedily became apparent that the animal was not entirely blind, but could see towards the right with the outer portion of its left eye. It noticed and winced at threats made towards the right, came forward and pecked at pieces of meat held in this position, though its aim was not very accurate, and one day pursued about the cage and ultimately, after considerable difficulty, captured a mouse, which it devoured whole. No doubt can therefore be entertained as to the binocular relations of each cerebral hemisphere in the owl. It is stated, however, by Michel, as well as by Singer and Münzer, that there is total decussation of the optic tracts in this bird. If this be correct, it follows that total decussation of the optic tracts is not inconsistent with binocular representation in each cerebral hemisphere.

My own experiments, as well as those of Munk, Horsley, and Schäfer, show that when the lesions are strictly limited to the visual sphere, vision alone is affected or abolished, without any implication of the other forms of sensibility, general or special, and absolutely without any motor paralysis. The contrary results obtained by some authors are without doubt dependent on primary or secondary injury to other sensory or motor tracts or centres. In Goltz's experiments the affections of vision from injury of the occipital regions appear to have been almost invariably associated with other forms of sensory disturbance; but the manner in which he established his lesions has not been sufficiently definite as to exclude implication of the sensory tracts of the internal capsule, or other sensory regions of the cortex. Whether after destruction of the whole visual sphere in the higher animals, man and monkey, any form of reaction to retinal impressions, beyond that of the pupil, may continue—as has been contended for by Goltz in the case of dogs, and by Luciani and Tamburini, and Lannegrace even in the case of monkeys—is not supported by clinical investigation, or by my own experiments, or those of

Munk on monkeys. Though the monkey, rendered blind by total extirpation of its visual centres, acquires the power of avoiding obstacles when left amidst its usual surroundings, yet this appears to be due rather to a sharpening of its other faculties, or more attentive appreciation of the impressions made on these by the objects with which it is surrounded, than to visual sensation. The question is, however, one which may well bear further investigation; for, if retinal impressions are co-ordinated with apparently purposive actions in the subordinate centres of the lower vertebrates, such as fishes, reptiles, and birds, there is at least the possibility that similar reactions may be discoverable in the higher animals, even though in a much less degree. It is certain, however, that the visual area of the cortex is not a merely functionally differentiated region capable of replacing, or of being replaced by, other cortical regions, inasmuch as destruction of the visual centres leads to atrophy in the primary optic centres, optic tracts, and optic nerves; and, conversely, destruction of the optic radiations leads to atrophy strictly confined to the regions included within the visual zone. The differentiation of an area exclusively—so far at least as can be judged from clinical and experimental results—would strongly favour the hypothesis that the other sensory faculties are also separately localised in definite cortical regions.

LECTURE IV.

LECTURE IV.

The Auditory Centre.

Mr. President and Gentlemen,—Among the reactions consequent upon electrical stimulation of the cortex there is one, or rather an assemblage of reactions, which might almost be considered of itself indicative of the existence of subjective auditory sensation—a reaction which guided me in my first attempts to define the auditory sphere by the destructive method. The reaction in question is that which occurs on irritation of the superior temporal convolution and its homologues in the lower vertebrates: namely, quick retraction or pricking of the opposite ear, associated frequently with opening of the eyes, dilatation of the pupils, and turning of the head and eyes to the opposite side. These are just the phenomena which occur when a shrill sound is suddenly made in a monkey's ear, as I have found by actual experiment. The reaction, however, varies somewhat in its completeness. After the first surprise is over, the repetition of the experiment always induces the pricking or retraction of the ear, but generally fails to induce the other parts of the reaction, namely, the intense look of surprise, and direction of the head and eyes to the supposed source of the sound. The results are still more characteristic on stimulation of the homologous region (14, Figs. 9—11) in those animals whose habits are such as to make their safety largely dependent on the acuteness of their hearing. The region in question is the posterior division of the third external or supra-Sylvian convolution. The reaction common to all these is pricking of the opposite ear, but the other factors vary in intensity. In the lop-eared rabbit, irritation of this region causes sudden elevation of the ear, as well as retraction and exposure of the mouth of the auricle towards the referred region of the sound. Occasionally the animal makes a sudden start and movement, as if to bound off the table. In the wild jackal, also, I observed on one or two occasions that the application of the electrodes to this region caused the animal to make a sudden spring or bound forward, pricking up both ears as if suddenly startled. If the movements of the eyeball on stimulation of the occipito-angular region are to be regarded as signs of arousal of subjective visual sensation, we have, I think, in the reactions under consideration, still more characteristic indications of the arousal of subjective auditory sensation. The determination, however, of affections of hearing is not so easy as that of sight in the lower animals. It is difficult to discriminate between mere reflex starting to sounds, and hearing proper. Nor is it easy to avoid mere coincidences, or to entirely avoid attracting the animal's attention by other channels of perception, such as sight, or smell, or sense of proximity conditioned by vibration, warmth, agitation of the air, and such like. The animal's present behaviour should be compared with its past, and with that of normal animals under conditions of variation of sound, all other things remaining the same. And even when all these precautions are taken, it is extremely difficult to avoid every source of fallacy. Hence it may happen, as it has actually happened, that different observers may arrive at different conclusions, and animals may be taken to be deaf which are not in reality so, simply because they do not respond to the test employed, or *vice versâ.*

In one of my earlier experiments, in which the upper two-thirds of the superior temporal convolution were destroyed on both sides, the following note was made as to the condition of the monkey the day after the operation.[1] "Sight was good and tactile sensation unimpaired. Various experiments were made to ascertain the existence or not of hearing, but it was not easy to devise a test, as the animal was continually on the alert, and it was not easy to make a sound without in any way attracting its attention by sight. The following method was tried: while the animal was sitting quietly by the fire I retired to the other room, and, while watching through the chink of the half-shut door, called loudly, whistled, knocked on the door, tinkled glass, etc., without ever causing it to look around or give any sign of having heard. I then cautiously approached the animal, and not till it saw me did it give any sign of consciousness of my presence. When the same experiment was repeated while the monkey and its companion were quietly seated at the fire enjoying the heat, it gave no sign of hearing, while its companion started with alarm, and came with curiosity to ascertain the cause of the sound. Ten

[1] Experiment XV, *Phil. Trans.*, vol. 265, Part II, 1875.

hours afterwards, in the presence of Dr. Burdon Sanderson, I repeated the various tests with the view of eliciting signs of hearing. To all it remained without response. It seemed unconscious of my presence when speaking close to its ear, and only started when it caught sight of me."

I recorded also four other experiments,[2] in which, along with destruction of other portions of the temporal lobe, the superior temporal convolution was invaded, unilaterally or bilaterally. In two of the cases (XI and XII), in which the temporal lobe was destroyed only on one side, there was impairment or total abolition of reaction to sound when the ear on the same side was plugged; and in the two other cases, in which the destruction was bilateral, no signs of hearing could be elicited during the short period which the animals were allowed to survive, though, in other respects, they were fully on the alert. In these experiments, however, the time that elapsed between the infliction of the lesion and the death of the animals was not sufficient to establish any very reliable data as to the permanency of the impairment of the sense of hearing, which was undoubtedly, however, affected in all for the time being. In my subsequent investigations, in conjunction with Professor Yeo, however, it was established in the first place by an extensive series of experiments on the temporal lobe[3] that no signs of impairment of hearing could be detected when every part of the temporal lobe was destroyed, except the superior temporal convolution. What appeared to us, and most of those who saw it, conclusive evidence of the relation of the superior temporal convolution to the sense of hearing, was the behaviour of a monkey in which both superior convolutions were actually or potentially destroyed by means of the cautery. Where the cortex was not absolutely removed, the grey matter was undermined, and the medullary fibres destroyed by the action of the radiant heat.

This monkey was exhibited before the assembled physiologists at the International Medical Congress in London in August, 1881, and was admitted by all to be deaf, so far at least as that could be determined by comparing its behaviour with that of a normal animal, to the explosion of a percussion cap in the room.

As questions were raised in regard to the actual condition of this animal before and after the operation by the experiments of Professor Schäfer, to which I am about to allude, I have published

[2] Experiments XI, XII, XIII, XIV, *op. cit.*, p. 462.
[3] *Philosophical Transactions*, Part II, 1884.

a full account of my notes and observations on this animal.[4] Briefly, these were as follows: in all other respects, except as to hearing, it was in a perfectly normal condition. During the first four days after the operation, no signs of hearing could be elicited by any sounds made in its vicinity, and which invariably attracted the attention of normal monkeys. While the other animals were observed eagerly listening to approaching footsteps, this animal made no sign of attention until the person came within range of vision. It was observed also that, at first at least, the ears of the animal did not twitch as they do in monkeys which undoubtedly possess the sense of hearing, but it was doubtful whether the absence of reaction in the ears continued during the whole time that the animal survived. Almost daily examination was made during the thirteen months that it was allowed to live. To sounds of various kinds, such as calling by name, to which it used always to respond, tapping, whistling, ringing of bells, shuffling of feet on the floor (a sound which normal monkeys are particularly quick to notice), this animal paid no attention. Occasionally, however, it seemed to start coincidently with loud sounds made in its vicinity, so that doubts were constantly being raised as to whether it was absolutely deaf or no. These reactions were considered to be probably mere coincidences, for in general it did not even start when a percussion cap was exploded near it. Six weeks after the operation, while the animal was disporting itself before the assembled physiologists at the Medical Congress, it paid no heed to the explosion of a percussion cap, while another monkey, exhibited at the same time, started visibly, as, in fact, did the whole audience. From this time onward the tests were constantly repeated and varied in every conceivable manner, but the results were essentially the same, and the conclusion seemed to be justified that the animal was essentially deaf, and that the occasional start which it made to loud sounds was either coincidence or merely of the character of the reflex start, which may occur in animals after removal even of the whole cerebral hemispheres.

Schäfer, in his earlier experiments, in conjunction with Horsley, did not arrive at any very definite conclusions with regard to the sense of hearing, though in one of their experiments[5] in which they had removed the right temporo-sphenoidal lobe, the animal did not seem to hear slight sounds when the ear on the same side

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[4] *Brain*, April, 1888, p. 13.
[5] Experiment 30, *Phil. Trans.*, 1880.

as the lesion was stopped. But, working with Sanger-Brown, he succeeded in removing all doubts which he might have entertained on the question, and in convincing himself that hearing was not in the slightest degree affected after complete removal, not only of the superior temporal gyri but of the whole temporal lobe itself on both sides. He thus describes the result of their experiments[6]:—

" In six monkeys we have more or less completely destroyed the superior temporal gyrus upon both sides. I say more or less completely because in one or two a small shred of grey matter belonging to this convolution was found *post mortem*, but practically the lesion was complete in all six, some of the grey matter within the fissures bounding the gyrus being all that could be taken to represent the convolution, and even this being deprived of its medullary centre. But in order to make assurance doubly sure we, in one monkey, a large female Rhœsus, separated up the fissures bounding the gyrus and scooped it out entirely from the very bottom of the fissures, so that not a trace of the convolution in question should remain. In all six cases the result was the same. Hearing was not only not permanently abolished : it was not perceptibly affected. The animals, even immediately after recovery from the anæsthetic, reacted to slight sounds of an unusual character such as smacking of the lips or the rustle of a crumpled newspaper. Some of them were under observation for several months, and there never was any doubt in our minds as to the full possession of their auditory faculties. Nor could the reactions they exhibited to sounds be explained by supposing that they only responded in a reflex manner, for they gave every evidence of understanding the nature of different sounds, such as that caused by turning a door-handle or the differences between the footsteps of different people, varying emotion being exhibited according to the anticipations (of food, etc.) which the sounds called forth."

Two of these animals, in which the destruction of the superior temporal convolution seems to have been most complete, were examined by several members of the Neurological Society. Two, who, however, did not record the tests they employed, were of opinion that the animal heard; while another thought on one occasion that one of the animals could hear, at another time that it seemed deaf on the left side, and, on still another occasion, that

6 *Brain*, Vol. 10, p. 373.

it did not seem to react to sound so readily and completely as a normal animal.[7]

As illustrating the difficulty of arriving at definite conclusions on this matter, one member of the Society thought that a perfectly normal monkey was quite deaf, and another that an animal in which both superior temporal gyri had been removed was also deaf. Schäfer[8] believes that I also was satisfied as to the existence of auditory perception in his animals. Such examination as I made of them did not, I think, furnish any unequivocal evidence on the point. An unaccountable discrepancy between Schäfer's results and Yeo's and mine thus appeared to exist. If in his animals hearing was not perceptibly affected by the double lesion, this certainly was not the case in ours; for there was no question as to the profound difference between it and a normal monkey, and the only doubt was whether it had any real sense of hearing at all.

In order, if possible, to clear this matter up I have lately re-investigated the question. In one monkey I removed, first, the whole of the convex aspect of the left temporal lobe, including the superior temporal gyrus. The animal speedily recovered from the unilateral operation, and, for the first few days, though undoubtedly it heard, it seemed to hear less distinctly towards the right than towards the left. A fortnight afterwards a similar operation was performed on the right side, but though the animal lived five days it remained in a state of great apathy. It took no notice of what was going on around it, and was altogether indifferent to the loudest sounds made in its vicinity. The experiment, therefore, on account of the short period of survival, was not quite a satisfactory one. Another monkey in which I performed the operation of bilateral extirpation of the superior temporal gyrus, with an interval of one month between the two operations, was specially well adapted for experimentation in regard to the sense of hearing. It was a remarkably tame dog-faced monkey, and its character and modes of behaviour under different circumstances were made the subject of careful study before it was operated upon. It was a noisy, talking monkey. It invariably responded when called to by name, and came immediately when called. It imitated smacking of the lips and other sounds of endearment. It always shouted vigorously and loudly when anyone approached or opened the door leading down

[7] See *Brain*, July, 1889, p. 164.
[8] *Phil. Trans.*, 1888, B. 30, p. 325.

to the laboratory in which it was kept. The rustling of a paper bag, from which it was accustomed to receive sweetmeats and nuts, was the signal for vociferous cries; as also any movement of the handle of a drawer in which apples and fruits were kept. It had an insatiable appetite, and was always clamouring for food, of which it never seemed to have enough. It had also an insatiable thirst, and the sound of plashing of water, made by turning

Fig. 16.

Fig. 17.

on the water-tap, caused it to shriek to be let out and put its mouth under the tap. Not a sound could be made in its vicinity, or a movement of its companion monkeys in the other cages, without exciting its active attention. It was full of fun and mischief, and in every respect an animal unusually adapted for determination of any alterations that might occur in respect of its auditory or other facilities. The left temporal superior convolution was scooped out on October 8th. (As will be seen in the photograph a small portion also of the middle temporal gyrus was destroyed, Fig. 16).

The next day, owing to the occurrence, as afterwards proved, of some recurrent hæmorrhage and tension in the wound, there were one or two slight epileptic seizures affecting the right side. These, however, ceased entirely when the wound was redressed, and the animal was speedily quite bright and active.

On the second day it turned its head to the dangling of keys close to its left ear, but it did not do so, or very doubtfully, to the same test applied to the right. Next day, and from that time onwards, it appeared, as regards its hearing, in every respect as it had been before the operation. It was noted, however, that it had become completely hemiopic to the right—a condition which lasted more or less completely until its death five months subsequently. This hemiopia proved after death to be due, in all probability, to the recurrent hæmorrhage, which occurred on the day after the operation, ploughing up the optic radiations in the occipito-angular region.

On November 5th, the superior temporal gyrus of the right side was similarly exposed and scooped out. This time the lower extremity of the gyrus almost entirely escaped (Fig. 17). On the following day the animal made no response to any sounds made in its vicinity, nor when the door leading to the laboratory was slammed, nor to the noise of footsteps on the stairs which formerly used to excite lively demonstrations.

On the third day, though otherwise alert and bright, it made no reaction to sounds of any kind, did not reply to calls, did not notice the noise of footsteps on the stairs, exhibited no sign of perception when the water-tap was turned on, though it was evidently intensely thirsty, as it drank eagerly when water was presented to it; paid no attention to the cries of two animals which were placed in the adjoining cage, and, in general, responded to none of the tests of hearing which formerly aroused its active interest.

On the seventh day the condition was essentially the same. It paid no heed when called to, or when the door leading to the laboratory was slammed. The rattling of the drawer in which the food was kept or the rustling of the paper bag containing the sweetmeats were altogether unnoticed; the plashing of water was unheeded; and it went on quietly with its occupation, eating or searching for food on the floor of its cage, while various sounds, such as springing a rattle, loud barking, whistling, etc., were being made, which startled the other animals in adjoining cages. On the tenth day the condition was essentially the same. There was no reaction to calls, shuffling of feet, etc., which caused other two normal monkeys in the adjoining cage to peer curiously. On this day a test was employed to which it formerly invariably responded. It was late in the evening. I put out the light in the laboratory and ascended the stairs and shut the door. Several times I opened the door and called the animal by name. One of the other monkeys called back in reply, but no response was made by this animal. On former occasions this was the signal for shrill and loud outcries. On the following day the same tests were repeated, and with the same results. It was very fond of the laboratory attendant, and would invariably go to him if he called it. On this day, while it was on the table and watching my movements, the laboratory attendant came down the stairs and, standing behind it, called it repeatedly. The animal paid no attention whatever, and never once turned its head in his direction.

On November 20th (fifteen days after the operation) the following notes were made:—

"The animal well and active, occasionally uttering grunts of satisfaction while sitting quietly by the fire. It also cries loudly when it wants food, but it never responds when called to; pays no attention to the familiar sounds, such as opening the drawer containing the apples or turning on the water tap, which formerly excited in it lively demonstrations. To-day a box containing a whistle, capable of being blown by a long india-rubber tube in such a manner as to avoid attracting the animal's sight, was placed in its cage and the whistle repeatedly blown, but it was absolutely unmoved. The same experiment with three other monkeys caused signs of alarm and perturbation."

About this time the question began to be raised whether the animal did not seem to be aware, by a sense of vibration or otherwise, of the approach of footsteps descending the spiral staircase leading into the laboratory. It was quite certain, however, that while it was being watched, and its attention thus occupied, it seemed quite unconscious of any sound made to divert it. On November 30th, that is, three weeks after the operation, these observations were confirmed after careful study by myself and assistant for several hours. But when all was still it seemed to be aware, as evidenced by its cries, of the proximity of anyone walking on the floor overhead, or opening the door leading down into the laboratory. This was noticed more particularly in the early morning, when this and the other monkeys were eagerly looking towards the stairs expecting their breakfast. Repeated observations during the course of the following week succeeded in clearing up the apparent irregularities in its reactions. It became evident that when the animal was left to itself it was aware of being called to, or of the sound of opening or slamming the door leading to the place in which it was kept, but when anyone was present in the laboratory, and the animal occupied in observing him, it showed no signs of hearing, and did not look round like the other monkeys when called to or when sounds of various kinds were made. If I waited in the laboratory within the range of the animal's vision, and my assistant went to the top of the stairs and called, it paid no heed whatever to anything he might do to attract its attention. Though it occasionally started when a percussion cap was exploded in its vicinity, it did not do so or look around if it happened to be engaged on anything else at the moment; whereas other monkeys would invariably start and look around towards the cause of the sound, and this condition remained practically unchanged until the death of the animal. In the direction of the laboratory door alone, towards which it was almost constantly looking, with expectation, did it seem able to refer sounds, but otherwise, especially when its attention was diverted in any way, it seemed entirely unaware of their origin, and did not turn its head in their direction. It either did not hear or wholly disregarded such sounds as scratching, tapping, rattling of keys, and so forth, which caused the other animals to peer eagerly through the bars of their cages. The plashing of water, rustling of paper, opening of the drawer from which it was accustomed to receive choice morsels never excited any notice, and caused none of the lively signs of interest which formerly were so characteristic. I did not observe in this animal, at least during the latter periods of observation, that absence of the twitching of the ears which I had noted in a previous experiment.

The condition of this animal may, therefore, be stated briefly as follows. At first it failed absolutely to respond to any of the tests which formerly excited active reaction, and which invariably attracted the attention of normal monkeys. To the last, with the single exception perhaps of the door of the laboratory from which it was always expecting something, it never realised the origin of sounds; it was altogether indifferent to sounds which formerly were full of significance to it, and all that could be said was that it was not, when otherwise occupied, insensible to sonorous vibrations. And it would have been difficult to make this out with any degree of certainty, had it not been that the animal was one qualified to give oral testimony of the fact. Whether this form of auditory sensibility is to be attributed to portions of the cortical auditory centres undestroyed by the lesions described, or to subcortical or mesencephalic centres, I am not yet in a position to decide. I have not yet been able successfully to carry out observations on animals in which the temporal lobes have been destroyed on both sides; but if, as Schäfer's experiments seem to indicate, the whole of the temporal lobes, like the other cerebral lobes, may be removed without entirely abolishing reaction to sounds, we should have reason for believing, with Longet, Goltz, etc., that in monkeys, as well as lower mammals, a crude and simple form of auditory sensation is still possible through the agency of the lower centres.

Munk, from his experiments on dogs, states that destructive lesion of the point B (Fig. 14), situated towards the lower extremity of the supra-Sylvian and adjacent extremity of the second external convolution, causes a condition as regards hearing similar to that resulting from destruction of A (Fig. 14) in the sphere of vision; a condition which he terms "psychical deafness" (*Seelentaubheit*). The dog seems to hear, but is unable to interpret the sound that it hears. This condition, however, lasts only for a few weeks at most. The animal again learns the meaning of sounds, and becomes restored to its normal state. In this region are stored up, according to him, the auditory pictures, similar to the visual pictures in the region A, (Fig. 14). Frequently, however, before the secondary disturbances created by the primary lesion have subsided, the animal appears to be totally deaf, so that it exhibits no reaction to any kind of sound, however loud. Occasionally when the whole of the cortex of both temporal lobes had been destroyed, he has observed persistent "cortical deafness" (*Rindentaubheit*), as he terms it, but as none of the animals on which he has performed this operation seem to have lived beyond a few days, his experiments do not afford data for the determination of the duration of this complete deafness. He, however, assumes that the auditory area of the cortex embraces a much larger extent than B, and includes, according to his figures, the whole of the posterior half of the third, and also of the posterior or lower divisions of the first and second external convolutions. With respect to the auditory sphere in the brain of the monkey, he assumes—for he does not appear to have performed any experiments bearing on this point—that it is situated at the lower extremity of the middle temporal gyrus (B., Fig. 18), a region which I have completely extirpated without causing the slightest affection of auditory sensation. And he considers that the upper portion of the superior or temporal gyrus (G, Fig. 18) is the sensory sphere of the ear; of this I can obtain no evidence, for neither after unilateral nor bilateral extirpation of this region have I been able to verify any affection of the sensibility of the auricle.

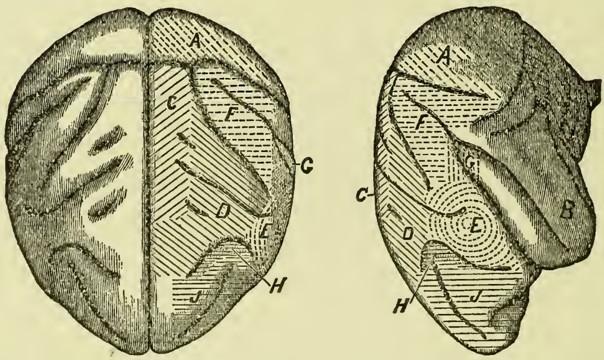

Fig. 18.—Cortical centres of the monkey, according to Munk. A, Visual area; C to J, tactile sensory areas (*Fühlsphaere*) of Munk; psychomotor areas of other authors; D, fore-limb region; C, hind-limb region; E, head region; F, eye region; G, ear region; H, neck region; J, trunk region. B is placed upon that portion of the cortex which, from experiments on dogs, is assumed to be the auditory area.

Luciani and Tamburini[9] found that unilateral destruction of the upper and posterior part of the third external convolution in dogs caused deafness in both ears, but to a greater extent in the ear of the opposite side. The difference in auditory sensibility on the two sides greatly diminishes, and after a few days disappears altogether, though it cannot be asserted that perfect recovery ever takes place. After comparative equalisation of the power of hearing on the two sides, removal of the corresponding region of the other hemisphere is followed by almost total deafness, approximately equal on both sides. This bilateral deafness passes off gradually, but data do not yet exist, according to them,

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[9] *Sui Centri Psico-Sensori Corticali*, 1879.

for determining whether perfect recovery takes place. When the destructive lesions are confined to the posterior part of the second external convolution, and do not implicate any part of the third, there does not occur the slightest impairment of hearing, which, indeed, sometimes appears to be unusually keen. These authors believe that semi-decussation of the auditory nerves exists similar to that of the optic nerves, and that both ears are represented in each cerebral hemisphere. This latter is undoubtedly the case; for unilateral extirpation never gives rise to permanent deafness of the one ear; but, though I have on many occasions, after extirpation of the auditory area in one hemisphere, observed loss or impairment of hearing in the opposite ear, I have never been able to detect the slightest impairment of hearing on the ear of the same side. Luciani[10] states: "The effects of extirpations in the province of the parietal lobe confirm what was recognised by Ferrier, and afterwards by Tamburini and myself, that the bend of the third external convolution certainly makes part of the auditory sphere in the dog, but demonstrate also that this sphere irradiates from its central point in the temporal lobe, upwards towards the parietal region, forwards towards the frontal, backwards toward the hippocampal, inward towards the cornu ammonis." He thus includes in his auditory sphere a large portion of the cortex which is concerned with other functions. In reference, however, to this and other sensory centres, Luciani appears to contend for a form of localisation which is no localisation at all, as every centre seems to perform to some extent the functions of every other centre; results which I regard as absolutely opposed by the facts of strictly localised lesions.

It will be observed, in reference to the position of the auditory area in the dog, that it does not occupy the same relation to the fissure of Sylvius that the superior temporal gyrus does in the monkey, but is separated from it by the posterior limb of the Sylvian convolution. It has been assumed by Meynert that the posterior division of the Sylvian convolution is the homologue of the superior temporo-sphenoidal gyrus.[11] I, however, have ventured to suggest that the resemblance between the posterior division of the Sylvian convolution and the superior temporal gyrus is only superficial, and is conditioned by the shallowness of the fissure of Sylvius. The investigations of Sir William

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[10] On the Sensorial Localisations in the Cortex Cerebri, *Brain*, 1885, p. 154.

[11] Die Windungen der convexen Oberfläche des Vorder-Hirns, *Archiv f. Psychiatrie*, Bd. vii, 1877.

Turner [12] have led him to the conclusion that the Sylvian convolution in the dog is in reality the homologue of the island of Reil, visible on the surface owing to the shallowness of the Sylvian fissure. In this case the posterior division of the supra-

Fig. 19.

Fig. 20.

Sylvian convolution would correspond accurately with that of the superior temporal gyrus.

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[12] Report on the Seals, *Challenger* Expedition, Part LXVIII, p. 124.

The occurrence of deafness from cerebral disease in man is unusual, owing to the extreme rarity of bilateral lesions affecting simultaneously both superior temporal gyri. There are, however, on record two important cases in which this double lesion occurred.

Shaw [13] has recorded the case of a woman, aged 34, who, two months before her admission into his asylum, lost power in the right arm, and soon after had a sudden apoplectic seizure, resulting in loss of speech and deafness. The loss of power in the right hand speedily passed off. She became excited, incoherent, and subject to delusions. On admission, she was found, after repeated testing, to be perfectly deaf and blind. Tactile sensibility and smell were unimpaired. She had occasional fits, and ultimately died of pneumonia a year after her admission. *Post-mortem* examination showed complete atrophy of the angular gyri and superior temporo-sphenoidal convolutions of both hemispheres. (See Figs. 19 and 20). The grey matter of the atrophied regions had entirely disappeared, leaving the outer layer attached to the pia mater, with a cavity underneath formed at the expense of the grey matter. The other cranial nerves were normal in appearance, but the optic nerves showed increase of the connective tissue septa, atrophy of the nerve fibres, and spaces filled with a colloid-like material. Whether the blindness was due to the lesion of the angular gyri alone or to degenerative changes in the optic nerves is a question, but the sudden onset of deafness in this case, coincidently with symptoms of cerebral lesion and the condition of the brain *post mortem*, point to the destruction of the superior temporal convolutions as its cause. A similar case has been reported by Wernicke and Friedländer: [14] "A woman, aged 43, who had never suffered from deafness or affection of vision, was attacked on June 22nd, 1880, with right hemiplegia and aphasia. She remained in the hospital until August 4th, when she was discharged. At this time the patient could speak, but she spoke unintelligibly, and was sometimes believed to be intoxicated. She not only could not make herself understood, but she could not understand what was said to her. She was received into the hospital again on September 10th, with slight paresis of the left arm. The right hemiplegia had entirely disappeared. The patient was looked upon as insane. She was absolutely deaf, so

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[13] *Archives of Medicine*, February 1882.

[14] *Fortschritte der Medicin*, Bd. 1, No. 6, March 15th, 1883; *Brain*, April, 1888, p. 19.

that she could not be communicated with. She died of an attack of hæmatemesis on October 21st. An extensive lesion was found in each temporal lobe, invading the superior temporal convolution on both sides. (See Figs. 21 and 22). The rest of the brain ex-

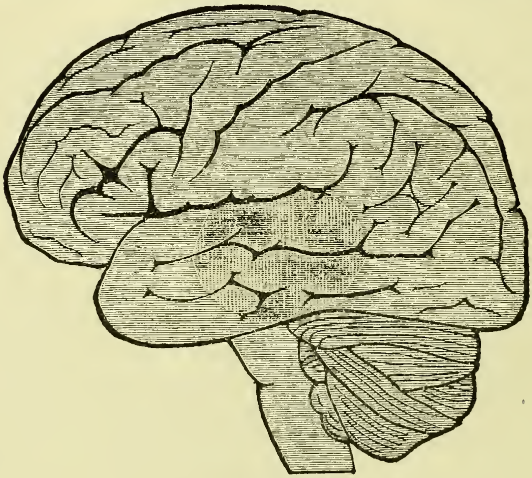

Fig. 21.

Fig. 22.

hibited no abnormality, nor were there any conditions leading to increase of the intracranial pressure or secondary affection of the cranial nerves.

It was proved that the patient had previously enjoyed excellent hearing. Her total deafness occurred suddenly in connection with the other indications of cerebral disease. In order to exclude possible local affection of the ears these organs were submitted to examination by Professor Lucae. The result of this examination was practically entirely negative, only a slight dry catarrh being found, and nothing locally to account for deafness. These authors conclude "that the auditory nerves ultimately end in the temporal lobe, and that double or bilateral lesion in these lobes causes complete deafness. It may therefore be stated with all certainty that the temporal lobes are the cerebral centres of hearing."

Though the lesions were not confined to the superior temporal gyri, yet these were involved both as to the grey matter and medullary fibres. The case, therefore, confirms, if it does not of itself suffice to indicate, the position I have assigned to the auditory centre in these gyri.

The affections of hearing with which we are most familiar in connection with cerebral disease are the various forms of what is termed "word-deafness"—a condition in which auditory ideation is impaired, more particularly as regards the association of articulate sounds with acts of articulation and things signified. The word-deaf is not devoid of auditory sensation, for he can hear the ticking of a watch, and can recognise and hum an air, but articulate sounds, except, perhaps, his own name or some simple combination of words, have no meaning, and cannot be repeated. Word-deafness has been found associated with affection of the superior temporal gyrus in the left hemisphere. Seppili[15] finds that of seventeen cases, in which a *post-mortem* examination was made, in every one there was lesion of the superior temporo-sphenoidal convolution, and twelve in which also the second or middle convolution was involved.

Of twenty-five cases of word-deafness of which I have notes, collected by Dr. Ewens, ten were from lesions of the temporal lobe alone. In seven of these the first temporal gyrus was particularly affected; in the remaining three, the exact limits of the lesion were not stated. Eight were from lesions implicating the angular as well as the upper temporal gyrus; six were from lesions invading the superior temporal gyrus and adjoining portions of the occipital or parietal lobes, and one was stated to have

[15] *Revist. Speriment. di Freniat*, vol. x, 1884.

been due to lesion of the angular gyrus alone. In this case there appears to have been both word-blindness and word-deafness. In all, therefore, except one, there was obvious lesion of the superior temporal convolution.

Further confirmation of the localisation of the auditory centre in this convolution is afforded by cases of auditory discharges or subjective auditory sensations in connection with irritative lesions implicating this gyrus. Gowers has reported two cases of this nature.[16] In the one a tumour, of which the oldest part was beneath the superior temporal convolution, caused convulsions commencing with an auditory aura referred to the opposite ear. In the other, a tumour affecting the superior temporal gyrus caused unilateral convulsions, preceded by a loud noise as of machinery. And Hughes Bennett[17] has reported several cases of auditory sensory discharges followed by temporary loss of hearing in the opposite ear, or in both. Thus a woman subject to epileptic attacks preceded by a loud noise like the ringing of a bell in the left ear, became temporarily deaf in each ear after each attack. Both ears were deficient in hearing, but the left undoubtedly the more so. The superior gyrus has also been found atrophied in cases of long-standing deafness or congenital deaf-mutism. Mills[18] records the case of a man deaf for thirty years; the brain, otherwise normal, showed extensive atrophy of both superior temporal gyri, more particularly on the left side. Broadbent[19] describes the brain of a deaf and dumb woman in which, in addition to some defect of the annectent convolutions and supramarginal lobule, there was atrophy of both superior temporal gyri more marked on the left side. The facts of human pathology, therefore, undoubtedly support the view that the sense of hearing is localised in the temporal lobe, and more especially in the superior temporal gyrus of this lobe.

The experiments of Baginsky,[20] as well as the microscopical investigation of Flechsig and Bechterew,[21] indicate that the auditory nerve is in relation with the auditory centre of the cortex through the lower fillet of the opposite side, and thence by means of the posterior tubercle of the corpora quadrigemina and corpus geniculatum internum with the medullary fibres of the cortex. Ba-

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16 *Diseases of the Nervous System*, vol. ii, p. 21.

17 Sensory Cortical Discharges, *Lancet*, 1889.

18 *University Medical Magazine*, November, 1889.

19 *Journal of Anatomy*. 1870

20 *Sitzungsb. Akad. d. Wissenschaften zu Berlin*, 1886, 12.

21 *Neurolog. Centralblatt*, December, 1886.

ginsky's experiments consisted in destroying the labyrinth in rabbits, and then tracing the course of the paths of degeneration thereby caused. He found a marked disappearance of the fibres of the lower fillet in the opposite side, and some degree of atrophy also in the posterior tubercle and brachium and corpus geniculatum internum. Von Monakow also states that, after extirpation of the temporal lobe in newborn rabbits, atrophy occurs in the corresponding medullary fibres of the internal capsule and in the corpus geniculatum internum of the same side; thus furnishing confirmation of the views of Baginsky and Flechsig.

We have thus grounds for believing that the central fibres of the auditory nerves do not, as Meynert has stated, all pass through the cerebellum on their way to the cerebral hemispheres—a hypothesis which is otherwise inconsistent with the results of destruction of the cerebellum itself. Some of the fibres of the eighth nerve undoubtedly pass into the cerebellum, but these appear to be the vestibular fibres from the semicircular canals, and not the cochlear or true nerve of hearing.

Centre of Tactile and Common Sensibility.

I will now proceed to consider the locality of the centres of common and tactile sensibility.

Many uncertainties still exist as to the paths and centres of the various forms of common sensation. It is universally admitted, since the classical experiments of Brown-Séquard, that, with the exception, perhaps, of the so-called muscular sense, the paths of all the other forms of sensibility are conveyed upwards on the opposite side of the spinal cord. But neither experimental, nor pathological, nor microscopical investigation has accurately determined in which particular part of the opposite side of the spinal cord the sensory tracts ascend to the brain. The experiments of Ludwig and Woroschiloff[22] appear to show that sensory impressions may be conveyed upwards, without any apparent disturbance of the normal relations, when the whole of the anterior and posterior columns, as well as the grey matter, has been severed; when, therefore, only the lateral columns of the cord remain intact. They found that, when only one lateral column remained, movements of the arms and

[22] *Der Verlauf motorischen und sensiblen Bahnen durch das Lendenmark des Kaninchens*, 1874.

anterior part of the body could be readily excited by irritation of the opposite leg behind the section, but only with difficulty by irritation of the leg on the same side. In order that impressions on the opposite leg should readily excite movements in the anterior part of the body, they found that that portion of the lateral column must remain intact which lies in the area bounded by the prolongation outwards of the anterior and posterior commissures, that is, the middle third. Ludwig and Woroschiliff were not able to differentiate the sensory from the motor tracts of the lateral columns, and concluded that both were more or less mingled together; but the facts of human and experimental pathology indicate that they are, to a large extent at least, distinctly separable from each other, and doubt may be entertained as to how far their experiments indicate the paths of true sensation as distinct from those of mere reflex reaction, more or less general. It does not appear that the paths of sensation proper degenerate upwards to any great extent after complete severance of the cord at any part. Of the paths which degenerate upwards the principal are the posterior median columns, or columns of Goll, which degenerate upwards, in some measure at least, as far as the nuclei graciles or post-pyramidal nuclei of the medulla oblongata. The posterior external columns, or columns of Burdach, degenerate upwards at most for a distance of only a few roots. In addition, upward degeneration occurs in the direct cerebellar tracts, which can be traced continuously to the restiform bodies, and thence into the superior vermiform process of the cerebellum. Anterior to the direct cerebellar tract, but more or less distinct from it, there is another tract in which ascending degeneration is frequently observed, as was first pointed out by Gowers, a tract which, as Bechterew has shown,[23] differs in its period of development from the other tracts of the cord. This constitutes the antero-lateral column. None of these tracts, however, have been conclusively shown to be the path of any form of sensation proper, using this term to distinguish the paths of conscious from those of mere afferent or centripetal impressions.

As the direct cerebellar tract undoubtedly ends in the cerebellum, and, as the observations of Tooth[24] would seem to show, is mainly derived from the posterior roots of the upper dorsal and cervical regions, and not from those of the lower extremities, we may eliminate these from the paths of sensation proper. The

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[23] *Neurolog. Centralblatt*, 1885.

[24] Secondary Degeneration of the Spinal Cord, 1889.

antero-lateral tract in which Gowers is disposed to place the path of painful impressions, appears, from the researches of Tooth, to consist largely of very fine fibres, and to arise from the cells of Clarke's column. It ascends to the nucleus lateralis, which is the upward continuation of the lateral horn of the cervical cord, also called the visceral horn. The further course of this tract is uncertain though its larger fibres are supposed by Tooth to ultimately reach the cerebellum. Gowers reports a case of unilateral lesion of the spinal cord[25] which would appear to support his hypothesis, and Bechterew states that analgesia follows transverse section of the anterior half of the cord. In neither of these observations, however, as Tooth remarks, can we eliminate affection of the grey matter itself.

I have lately performed an experiment on a monkey in which I divided the convex or outer half of the lateral column in the middle of the dorsal region. (Fig. 23.) Though a slight amount of paralysis occurred on the limb of the same side there was no

Fig. 23.

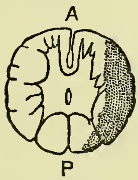

Fig. 24.

Fig. 25.

impairment of tactile or painful sensibility on the opposite leg the day after the lesion. The slightest touch on either limb immediately attracted the animal's attention. In another, in which I divided the greater portion of one half of the cord, excluding the posterior column, part of the anterior column, and that portion of the lateral column lying in the angle formed by the anterior and posterior cornua (Fig. 24), there was almost complete motor paralysis in the leg of the same side, but sensibility was not abolished on the opposite side. Whether sensation was at all impaired could not be determined with certainty, but the sense of pain was undoubtedly retained. These experiments are, therefore, opposed to the hypothesis that the antero-lateral tract is the path either of tactile or painful sensation.

In another experiment which I performed on a monkey, the particulars of which I have elsewhere recorded,[26] I divided the

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[25] Clinical Society's *Transactions*, vol. xi, 1877.
[26] Hemisection of the Spinal Cord, *Brain*, vol. vii, p. 1.

whole of the left side of the cord with the exception of the anterior and posterior median column. Though the greater portion of the left posterior median column and the whole of the right posterior median column, as well as the grey matter on the right side, and that surrounding the central canal on the left side were intact, there was complete anæsthesia and analgesia on the opposite side of the body. This experiment, therefore, negatives the hypothesis that the posterior columns are the paths of tactile sensibility. It also is opposed to the hypothesis that the posterior median column is the path of the so-called muscular sense on the same side. For the behaviour of this animal indicated, so far at least as can be judged from the observation of the lower animals, that it had entirely lost muscular sense on the opposite limb; for while it was able to move its right leg volitionally in all directions, and for all purposes, without any appearance of uncertainty or ataxy, and could grip strongly with its foot, this was only when vision was free. When, however, the eyes were blindfolded the animal was utterly unable to extricate its leg from any opposition to its intended movements.

In another experiment I endeavoured accurately to divide the posterior median columns in the mid-dorsal region. The lesion was effected by plunging a triangular keratome into the posterior median fissure to such a depth—as I had calculated by repeated experiments on the dead spinal cord—as would divide the posterior median columns down to the posterior commissure. Though it seemed as if the whole of the columns should have been severed, I could not after death verify greater destruction than of the portions immediately adjoining the median fissure. (Fig. 25.) Though the animal was for a few hours somewhat weak or awkward in its hinder extremities, next day not the slightest impairment of tactile or muscular sense could be discovered. It ran about without any sign of ataxy, climbed with its customary freedom, clambered down the bars of its cage, planted its feet with precision and without the aid of vision, and was at once aware when its feet reached the ground. The slightest touch on either foot, or on any portion of the lower part of its body, at once attracted its attention.

Bechterew has also found[27] that section of the posterior columns in the cervical region in dogs causes no loss of tactile or muscular sensibility, though the operations appear to be followed by disorders of equilibration. These, however, tended to disappear with

27 *Neurolog. Centralblatt*, February 1st, 1890.

the lapse of time. Bechterew's experiments, therefore, are opposed to the view that the posterior columns are the paths of any of the forms of sensation proper.

It has been stated by Brown-Séquard, and generally accepted by physiologists and pathologists, that the paths of the muscular sense do not cross with the other sensory tracts, but ascend in the cord on the same side; so that in hemisection or unilateral disease of the spinal cord, the muscular sense is impaired or lost on the side of the lesion and retained on the opposite and otherwise anæsthetic limb. The facts of hemisection of the spinal cord in the monkey are, in my opinion, opposed to this hypothesis, but I am ready to admit that experiments on the lower animals, in which we can only infer as to the conditions of consciousness, are not so satisfactory in this relation as accurate observations on human beings. On investigation, however, of the cases which have been adduced in support of Brown-Séquard's contention, I find that the evidence of the retention of muscular sense on the otherwise anæsthetic limb, and its impairment or loss on the side of lesion, is far from satisfactory.

Out of 43 cases [28] of apparently unilateral disease of the spinal cord in which, however, there were only two *post-mortem* examinations, in only 24 was there any mention of the condition of the muscular sense in the original papers. In 6 the only evidence given of the muscular sense being retained was the ability to perceive strong pressure, or the power of directing movements with precision:—a condition, however, which has been proved to be possible in the entire absence of any sense of movement. In 4 the method of testing the muscular sense is not stated. In 1 muscular sense appeared to be normal on both sides, no further details being given. In another the only note was that the paralysed limb did not judge as exactly as the other side difference in weights. In 3 the muscular sense [29] was present on the otherwise anæsthetic side, but in these three tactile sensibility was not lost. In one case [30] muscular sense appeared to be lost on the paralysed leg; but in this case there was some anæsthesia of the arm on the same side, and probably, therefore, also on the leg. In one no investigation seems to have been made of the muscular sense while the limb was paralysed. Afterwards it was said to have a certain degree

[28] Most of these cases have been quoted by Brown-Séquard in the *Archives de Physiologie*, vol. 1 and 2.

[29] Perroud, *Journ. de Méd. de Lyon*, vol. ix, 1868; Gilbert, *Archives de Neurologie*, tome 3, p. 275; Bayne, *Lancet* ii, 1865, p. 117.

[30] Brown-Séquard, *Lancet*, vol. ii, 1868, p. 689, Case 2.

of inco-ordination and loss of notion of position. In another[31] the only note was that the patient retained the power of estimating weights and the consistency of bodies on the anæsthetic limb. The state of the other was not mentioned, and no exact details are given as to the condition of the various forms of sensibility. Of the remaining cases, in one muscular sense was lost on the anæsthetic side.[32] The condition of the other is not recorded. In another[33] the conditions varied according to the progress of the disease, but the muscular sense was always retained on the anæsthetic limb, so long as tactile sensibility and the power of localisation were unaffected. In the third[34] muscular sense was retained on the paralysed limb, though its condition on the otherwise anæsthetic limb was not mentioned. This was the only case which was followed by a *post-mortem* examination. In another, Köbner's case,[35] it was found, on applying proper tests to the paralysed limb, that the patient had a perfect knowledge of any movement passively communicated to it; and a similar case has been recorded by Jaccoud.[36] Though, therefore, there appear to be some facts in favour of Brown-Séquard's theory, others are absolutely opposed to it. So that clinical observation hitherto cannot be said to give unqualified support to the theory that the muscular sense remains unaffected when all the other forms of sensibility have been lost. Such being the state of the question, the particulars of the following case, which I have recently had under my observation, are of some importance.

W. S., aged 25, admitted as an out-patient at the National Hospital for the Paralysed and the Epileptic on March 21st, 1890. Previous health had been good until three years ago, when he contracted syphilis. At Christmas, 1888, he observed that he had difficulty in emptying his bladder. Soon after this he had temporary paralysis of the sphincters, both of the bladder and rectum. In April, 1889, he complained of weakness of the left leg, which passed off after a few months, at the end of which time the right leg became affected and has continued so, becoming more and more rigid up to the present date. On examination, there is tenderness to percussion from the tenth to the twelfth dorsal vertebra, and to a lesser extent for some distance above this point. The patient com-

[31] Dundas, *Edin. Med. Journ.*, 1825, p. 304.
[32] Sir Charles Bell's case, *Nervous System*, p. 245.
[33] McKenzie's case, *Lancet*, 1883, vol. i, p. 995.
[34] Charcot and Gombault, *Archives de Physiol.*, vol. v, p. 144.
[35] *Archiv f. klin. Med.*, 1877, p. 208.
[36] *Leçons de Clin. Med.*, 1867, p. 451.

plains of constriction round the abdomen, just above the umbilicus. There are no abdominal or cremasteric reflexes on the left side, but both are present and well marked on the right. Condition of the limbs: The right leg is paretic and rigid. The knee-jerk is greatly exaggerated, and there is well marked ankle clonus. In this leg all varieties of sensation are normal. When his eyes are closed, he can indicate with perfect accuracy every movement that is communicated to his limb. There is weakness of the left leg, and the knee-jerk is increased. There is no complete analgesia, but there is absolute tactile anæsthesia from the foot up to the knee, and dulled from this to the level of the umbilicus. Sensibility to heat and cold is very much impaired. With his eyes closed he is absolutely unable to say in what position his limb or any part of his limb is placed, but he is able to direct its movements with fair precision.

In another case, the patient suddenly became paralysed on the left leg, and anæsthetic on the right. This fact he discovered by the insensibility of the leg to hot water which he could not bear with the right. At the date of my examination, a month after the attack, he had recovered from the motor paralysis of the left leg, but he was still absolutely insensible to thermal and painful stimuli on the right leg. Tactile sensibility was, however, equally good on both sides, and with it the muscular sense was also perfect in both.

To my mind the evidence, from the various facts mentioned, is in favour of the view that the whole of the sensory paths pass up the opposite side of the spinal cord, and that they are not contained either in the posterior median column, or in the direct cerebellar tract, or in the antero-lateral tract; and, as the pyramidal tract may be entirely sclerosed without any affection of sensation, we are led by a process of exclusion to suppose that the sensory tracts ascend in immediate relation with the central grey matter. If the sensory tracts retain constant relation with the grey matter, this would account for their non-degeneration upwards like the other continuous afferent tracts of the cord.

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LECTURE V.

LECTURE V.

Mr. President and Gentlemen.—Followed upwards in their course to the brain, clinical and pathological investigation would appear to show that in the medulla and pons the sensory tracts run in the fillet, or formatio reticularis. Those tracts — namely, the posterior external and posterior median—which do not decussate in the cord, decussate through the nuclei graciles and cuneati into the inter-olivary layer, and thence into the fillet and reticular formation (Edinger). Higher up, the evidence is in favour of the continuation of these tracts in the tegmentum of the crus cerebri, and thence into the posterior part of the internal capsule, whence they radiate outwards, according to Flechsig, and distribute themselves to the cortex in the region lying between the fissure of Rolando and the occipital lobe. It has been supposed by Meynert that the outer third of the foot of the crus is the path by which the sensory tracts of the spinal cord pass into the internal capsule; and in favour of this view is the fact that descending degeneration, while frequently found in the other fibres of the foot of the crus, has not usually been found here. Bechterew and Rossolymo,[1] however, have reported cases of degeneration of this part of the crus apparently in relation with lesion of the temporal and occipital lobes, and it is held by Flechsig that these fibres do not enter the internal capsule, but bend downwards and outwards to radiate in the cortex of the occipital and temporal regions. They are supposed to connect these regions with the cerebellum through the intermediation of the grey matter of the pons, but this is a point which, I think, stands in need of further investigation. In order, if possible, to throw light on the functions and connections of this part of the crus, I have recently divided it in three monkeys. The operation is a somewhat severe one, but the crus can be com-

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[1] *Neurolog. Centralblatt*, No. 7, 1886.

paratively easily exposed to view after removal of the lower portion of the temporal region. In all three animals the lesion was satisfactorily established, but none of them recovered sufficiently from the operation to enable me to make altogether reliable observations. But in none of them was there total loss of reaction to sensory stimulation, or greater impairment than could be accounted for by the cerebral lesion. So far as they go, therefore, the experiments are opposed to the view that the outer third of the foot of the crus is the path of the sensory fibres from below.

That the sensory tracts lie distinct from the motor in the posterior division (or rather posterior third of the posterior segment) of the internal capsule has been amply proved by the experiments of Veyssière[2] and by the researches of Charcot, etc., on cerebral hemianæsthesia occurring in man. The sensory tracts being admittedly distinct from the motor in the internal capsule, the question then arises whether these, which up to this point have maintained their separate position, fuse in the cortex with the motor, —as some believe—or are distributed to a special region.

In my earlier researches I had observed that tactile and common sensibility appeared to be entirely unaffected, notwithstanding the most extensive lesions of every portion of the convex aspect of the hemisphere, but I noted in several instances in which the destructive lesions extended deeply into the temporal lobe that sensibility became impaired or abolished on the opposite side of the body. Careful *post-mortem* examination showed that in all these cases the hippocampal region (including cornu ammonis and gyrus hippocampi) was more or less extensively invaded. These facts pointed to the hippocampal region as being the centre of common sensibility, and I therefore devised experiments by which I might reach and destroy this region by itself. On account of its deep-seated and concealed position this is, however, practically impossible, and it therefore can only be reached by methods which involve a greater or less extent of injury to the occipital lobe, or the lower temporal region. The effects of lesions of these regions can, however, be allowed for and eliminated, and any further symptoms than can be ascribed to them can be connected with those inflicted on the hippocampal region. The method which I followed in my earlier experiments was to break up and destroy the hippocampal region by means of

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[2] *Recherches Cliniques et Experimentales sur l'Hémianesthesie de Cause Cérébrale*, 1874.

a wire cautery thrust through the occipital lobe, and directed downwards and forwards in the course of the descending cornu of the lateral ventricle. In this manner I succeeded primarily or secondarily in entirely destroying the hippocampal region and its medullary connections without inflicting injury on the crus cerebri or neighbouring structures. The diagram before you[3] is an accurate representation of the superficial appearance of the lesion in one of these cases, and the track of the sinus made by the cautery. The result of this operation was anæsthesia and analgesia of the opposite side of the body, there being total or almost total absence of response to any kind of sensory stimulation. The limbs were not paralysed as to motion, but they appeared to be used with difficulty and awkwardness, and the feet tended constantly to slip off the perch when the animal shut its eyes and went to sleep. In none of my earlier experiments were the animals allowed to live for any length of time, as I considered it necessary to kill them as soon as the symptoms were clearly defined in order to avoid complication by secondary extension of the lesion, antiseptic surgery not being at this time in vogue. The lesion in this case was shown[4] to be strictly limited to the hippocampal and occipito-temporal region, and without any implication whatever of the internal capsule or crus cerebri. These experiments did not furnish any data towards the determination of the permanency of the symptoms, but they were sufficient to indicate a region, if not the whole region, related to the tactile, common, and apparently the so-called muscular, sensibility of the opposite side of the body.

I renewed my investigations on this subject at a later date[5] in conjunction with Professor G. F. Yeo. The method of performing the experiments was partly the one I had previously followed, namely, the destruction of the cautery, and partly that of cutting in towards the hippocampal region from the convex aspect of the temporo-sphenoidal lobe. Ten experiments in all were performed, and in five of these in both hemispheres. The result of this series of experiments confirmed in every particular those I had already arrived at, and showed that tactile sensibility was in every case impaired or abolished, in proportion to the destruction of the hippocampal and inferior temporal region. Unfortunately, none of the animals in which the destruction was complete, and

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[3] See Fig. 105, *Functions of the Brain*, p. 329.
[4] See Figs. 107 and 108, *Functions of the Brain*, p. 331.
[5] *Phil. Trans.*, Part ii, 1884, Experiments 24 to 33, Figs. 103 to 131.

the anæsthesia absolute, survived many days, so that the question of duration still remained unsolved. But it was established that a very extensive lesion might be made in one or both hippocampal regions without producing permanent anæsthesia. I need not enter into the details of all these experiments. The two following will suffice.

In one experiment [6] the left hemisphere was exposed and the whole of the inferior temporal convolution and hippocampal region were severed and scooped out, the lesion being such as to leave only the internal margin of the gyrus hippocampi with the tænia semicircularis and the fimbria of the fornix intact. Only a portion of the hippocampal gyrus included between the calcarine and collateral fissure (lingual lobule) remained. The result of this experiment was most marked. There was on the right side complete insensibility to thermal stimulation of such intensity as to cause the most lively signs of sensation on the left side, and total insensibility to every form of mere tactile stimulation, such as touching, gentle pricking, rubbing etc. The limbs were capable of being freely moved volitionally, but they were planted with great awkwardness and uncertainty as to position. While the animal was resting quietly with its eyes shut, I drew the right arm away from its side, of which fact it seemed unaware until it tumbled over. It was keenly sensitive to every form of stimulus, however slight, on the left side. Hearing was unimpaired in both ears; vision, however, seemed somewhat indistinct, though not abolished, towards the right. (This is an important fact in relation to the occurrence of hemiopia from lesion of the occipito-temporal region discussed above.) There was anæsthesia of the right nostril. The symptoms remained unchanged on the second day after the operation, the animal being otherwise in apparent good health, but on the third day it died suddenly of secondary hæmorrhage. A series of microscopic sections of the brain showed that, with the exception of the injuries, above described, in the inferior temporal and hippocampal region, the basal ganglia, crura cerebri, and other structures were perfectly intact.

In another animal a similar lesion was established, involving almost complete detachment of the hippocampal and lower temporal region from the rest of the hemisphere. In this animal there was at first almost, if not total, analgesia, and absolute anæs-

[6] Experiment 27, Figs. 125, 132, *op. cit.*

thesia to all gentle forms of tactile stimulation over the whole of the right side of the body. Hearing was unimpaired, but vision was somewhat defective towards this side, the animal appearing to have some degree of uncertainty as to the position of things offered it on the right front. The condition remained practically unchanged on the third day, when the animal had a slight right-sided fit, indicative of some irritation, found after death to be slight recurrent hæmorrhage. After this the analgesia became absolute, and no sign of perception could be obtained to any form of tactile stimulation. There was also total insensibility to tickling of the right nostril. A similar stimulation of the left caused active grimaces and signs of uneasiness. The animal could move its limbs freely and lay hold of objects firmly with the right hand, but it continually fell over on the right side, owing to the awkward and uncertain manner in which it planted its limbs. Death occurred on the fourth day. The lesion was found accurately limited to the lower temporal and hippocampal region of the left hemisphere without the slightest implication of the crus or basal ganglia. These experiments proved that the various forms of sensation embraced under the term common or tactile sensibility, including cutaneous, muco-cutaneous, and muscular, are capable of being profoundly impaired, or altogether abolished, for the time at least, by destructive lesions of the hippocampal region, and that the degree and duration of the anæsthesia varied with the completeness of destruction of the region in question.

The subject was next taken up by Horsley and Schäfer,[7] who, so far as I am aware, are the only physiologists who have repeated my experiments in this direction.

Horsley and Schäfer were at first unable to corroborate my observations, but I was able to demonstrate to them that this depended on the incompleteness of their excisions of the hippocampal region, and I assisted them in some of the experiments which they further prosecuted with excellent effect. In one animal in which the hippocampal region was removed there was on the following day partial analgesia, and complete insensibility to mere contact on the opposite side. Death, however, occurred on the second day, so that no conclusions as to duration were possible in this case.

In a second experiment, the hippocampal region was again removed, and the incisions made so as to detach also the margin of

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[7] Functions of the Cerebral Cortex, B. 20, *Phil. Trans.*, 1888.

the calcarine fissure and hippocampus minor. This animal was profoundly anæsthetic on the opposite side, but there did not appear to be absolute analgesia. All mere tactile stimuli, however, like touch, scratching, rubbing, gentle pricking, were absolutely unperceived, while similar stimulation on the other side at once attracted attention. Tactile anæsthesia continued for several weeks without appreciable alteration, but a gradual improvement occurred, so that examination at the end of six weeks revealed only some degree of impairment, as evidenced by less easily excited attention by gentle pricking, rubbing, etc., of the side opposite the lesion, as compared with the other. Severe pricking, pinching, or pungent heat, however, appeared to be well perceived. The gradual diminution of the anæsthesia, at first induced by extensive, if not complete, removal of the hippocampal region, led me to suggest similar experiments on the gyrus fornicatus, on the ground that the tactile centre might extend into the rest of the falciform lobe, of which the hippocampal region was only a part. This originated their experiments on the gyrus fornicatus, which proved the accuracy of Broca's anatomical views as to the unity of the falciform lobe, and demonstrated that lesions of the gyrus fornicatus caused similar symptoms to those produced by destruction of the hippocampal region, of, perhaps, even greater intensity and longer duration. In one of the experiments at which I assisted the animal in which, some weeks previously, the hippocampus had been removed, and which had completely recovered from any anæsthesia which might have existed immediately after the operation, the same hemisphere was again exposed and the region of the longitudinal fissure and the gyrus fornicatus excised along the whole length of the corpus callosum. The effect of this operation was to cause absolute analgesia on the opposite side, continuing several days after the operation, as well as complete insensibility to all milder forms of tactile stimulation. The analgesia diminished somewhat as time went on, but six weeks after the operation it was still manifest in some degree. The tactile anæsthesia was, however, apparently in no wise improved, all gentle forms of tactile stimulation being absolutely unperceived. The animal was in perfect health, and exhibited no indications of motor disorder; though, directly after the operation, there was slight weakness of the opposite leg, owing to the injury to the postero-parietal lobule and neighbourhood during the operations necessary to expose the gyrus fornicatus.

Many other experiments were made by Horsley and Schäfer, and recorded in their memoir in the *Phil. Trans.*, *sup. cit.*, and they sought also to determine whether there were any parts of the limbic or falciform lobe especially related to particular regions of the opposite side. They conclude from their experiments: "We have found that any extensive lesion of the gyrus fornicatus is followed by hemianæsthesia more or less marked and persistent. In some cases the anæsthetic condition has involved almost the whole of the opposite side of the body, in others it has been localised to either the upper or the lower limb and to particular parts of the trunk, but we have not yet succeeded in establishing a relationship between special regions of the body and the parts of the convolution which have been destroyed. Moreover, the anæsthesia was frequently very pronounced and general during the first three or four days after the operation, and, indeed, in several instances took the form of complete insensibility to both tactile and painful impressions, so that even a sharp prick or the contact of a hot iron would produce no indication of sensation, but after that time this general condition would become gradually in great part recovered from, or more localised in definite regions. In all cases, however, in which the diminution of sensibility was well marked during the first few days, it has persisted, although with lessened intensity, for many weeks in those instances in which the animals have been preserved for so long. In other cases, in which apparently the lesion was slight, the diminution of sensibility, although at first well marked, subsequently disappeared entirely. In some instances the hemianæsthesia took the form of inability (or diminution of ability) to localise the seat of irritation, whilst in one case, in which diminution of sensibility was exhibited in a very striking manner, the irritation, when rendered sufficiently intense for the monkey to become conscious of it, was responded to by the animal scratching a different part of its body from that to which the stimulus was applied."

Fig. 40 A [8] represents the condition of the right hemisphere of an animal in which the lesion indicated produced at first complete analgesia, followed by partial anæsthesia, lasting for ten weeks, at which time the animal died from an operation on the left. Fig. 42 [9] represents the brain of an animal in which the anterior two-thirds of the left gyrus fornicatus were removed. For a few days there was complete analgesia. A week after the

[8] *Op. cit.*
[9] *Op. cit.*

operation the condition was much improved, and at this time there was reaction over the whole of the right side to painful impressions, but often want of localisation of the seat of these impressions, a totally different part being scratched from that which was stimulated. Recovery gradually proceeded, so that after a time the difference of sensibility of the two sides was hardly perceptible, except about the arm and shoulder and in the foot. Eleven weeks after the first operation the right gyrus fornicatus was exposed and injured by scratching its surface with a needle. This, however, produced no perceptible result, and after a fortnight the animal was killed.

Fig. 43[10] represents the brain of a monkey in which the posterior part of the left hippocampal gyrus was destroyed. The result was great diminution of reaction to tactile and painful stimuli over the posterior part of the right side of the body, with slight diminution over the whole side.

It is not unlikely that, besides representing sensibility of the opposite side of the body generally, certain parts of the falciform lobe may represent more particularly the sensibility of special regions. But, though I occasionally noted in my experiments on the hippocampal region—like Horsley and Schäfer in their experiments in the gyrus fornicatus—that it seemed as if one region had been more affected than another, yet this was at times not apparent, and in general the anæsthesia has affected the whole of the opposite side, face, arm, leg, and trunk. Evidence is, therefore, so far, not conclusive of the existence of any altogether specialised centres in this general area. It is probable, however, that a certain degree of localisation may be established through the associating fibres, which undoubtedly connect this region with the motor centres of the cortex.

It has not yet been found possible to produce total persistent loss of all forms of tactile and common sensation on the opposite side after destructive lesions of the falciform lobe, but this may be due to the fact that this lobe has never been absolutely destroyed throughout its whole extent. It is probable, however, that common sensibility may, to some extent at least, be bilaterally represented, so that a certain amount of compensation may be effected by the falciform lobe of the other hemisphere. The paths of connection between the falciform lobe and the sensory division of the internal capsule have not yet been traced by any

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[10] *Op. cit.*

anatomist, but in view of the proofs which have been above given of the relation between the falciform lobe and tactile and common sensibility, it is obvious that the hypothesis of Flechsig as to the distribution of the sensory tracts in the parietal lobe, requires amendment. No scheme of the cortical distribution of the sensory tracts can be admitted as correct which does not connect them with the cortex of the callosal and hippocampal convolutions. Though the gyrus fornicatus appears to be a purely sensory region, and, therefore, one destruction of which should not give rise to centrifugal degeneration in the spinal cord, France[11] has found, apparently in relation with destruction of the gyrus fornicatus, secondary degeneration of the pyramidal tracts of the crus cerebri and spinal cord. It is, however, to be noted that in most, if not all, of the cases in which the gyrus fornicatus was destroyed, either the marginal gyrus or neighbouring motor centres and tracts were also more or less implicated, and the suspicion arises that the descending degeneration is in reality due to this cause. France, however, believes that the degeneration occupies a different region of the pyramidal tract from that resulting from lesion of the marginal gyrus alone, being in the latter case towards the posterior and outer part of the crossed pyramidal tract, in the former occupying the whole sectional area of the same.

These considerations are not, however, sufficient to remove all doubts; and these are emphasised by the fact that lesions of the hippocampal division of the falciform lobe, sufficiently far removed from the motor centres and tracts as to ensure their freedom from injury, lead to no degeneration of the pyramidal tracts. The question is one which requires further investigation.

Olfactory and Gustatory Centres.

The position of the olfactory centre, or at least its principal portion, may with great probability be inferred from the cortical connections of the olfactory tract, altogether apart from physiological experiment. The chief and, in man, the only constant connection of the olfactory tract with the hemisphere is the so-called external root, which passes outward across the anterior perforated space to the cortex of the hippocampal lobule, or anterior

[11] Descending Degenerations which follow Lesions of the Gyrus Marginalis and Gyrus Fornicatus in Monkeys, *Phil. Trans*, B. 48, 1889.

and lower extremity of the hippocampal gyrus (see Fig. 26, *Trol.*). Owing to the original formation of the olfactory bulb and tract as a diverticulum from the anterior cerebral vesicle, the cavity of which has become almost entirely obliterated, the remnants of its original connection with the mesial, external, upper, and lower aspects of the cerebral hemisphere are still spoken of as roots of the olfactory tract. Though in man and the monkey all the said

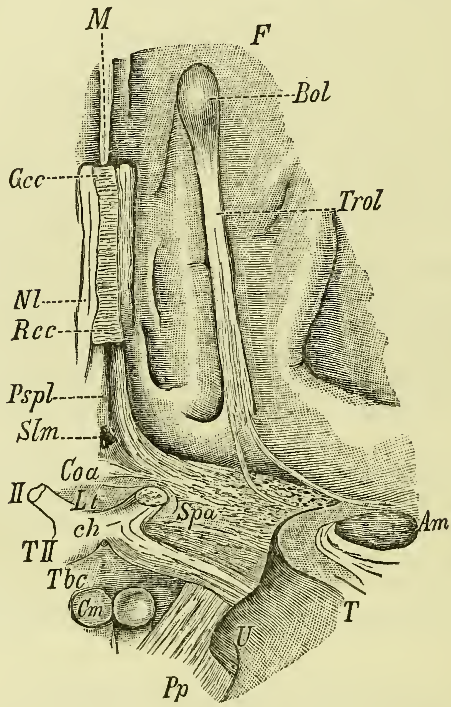

Fig. 26 (after Obersteiner).—*Pp*, pes pedunculi; *Cm*, corpus mammillare; *Tbc*, tuber cinereum; *TII*, tractus opticus; *ch*, chiasma; *II*, nervus opticus; *T*, temporal lobe; *U*, uncus; *Am*, nucleus amygdalæ; *Spa*, substantia perforata anterior; *Lt*, lamina terminalis; *Coa*, anterior commissure; *Pspl*, pedunculus septi pellucidi; *Slm*, Sulcus medius subst. perf. ant.; *Rcc*, rostrum corporis callosi; *Gcc*, genu corporis callosi; *Nl*, nervus Lancisii; *M*, longitudinal fissure; *F*, frontal lobe; *Bol*, bulbus olfactorius; *Trol*, tractus olfactorius.

roots, except the external one, are practically obliterated, yet in other animals, in whom the sense of smell is largely developed, four roots are usually described, namely, an external root passing to the hippocampal lobule; a superior and middle root, connecting the tract respectively with the grey matter of the base of the frontal lobe and the trigonum olfactorium, or grey matter of the anterior perforated space; and an inner root, which appears to fuse with the anterior extremity of the callosal gyrus. The connections of the olfactory tract, by means of its inner and outer root, with the anterior and posterior extremities of the falciform lobe, have been compared by Broca to a tennis racquet, of which the circumference is formed by the falciform lobe and the handle by the olfactory tract and bulb (see Fig. 27).

According to the development of the sense of smell in different animals, the structures above described, or parts of them, undergo great variations. Broca divides all animals into two classes—first,

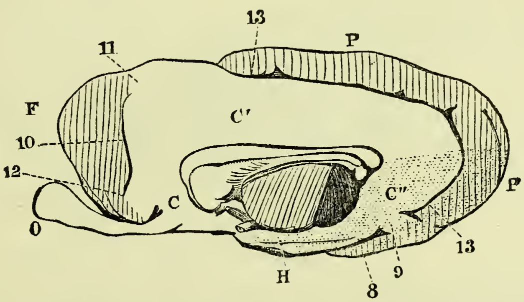

Fig. 27.—Inner surface of the right hemisphere of the Otter (Broca). O, olfactory lobe; H, hippocampal lobe; C, commencement of the lobe of the corpus callosum; C, C′, C″, lobe of the corpus callosum; F, frontal lobe; P, P, parietal lobe; 8, limbic fissure; 9, pli de passage rétro-limbique; 10, subfrontal sulcus; 11, pli de passage fronto-limbique; 12, inferior fronto-limbic annectent gyrus; 13, subparietal fissure.

the "osmatics," a class which includes the great majority of mammals, and, secondly, "anosmatics," in which the sense of smell is relatively feebly developed, including (primates, amphibious carnivora), rudimentary (balænidæ), or altogether wanting (delphinidæ). In the osmatics, as you may see in the specimens before you, the olfactory bulb and tract are large, and the hippocampal lobule in particular attains extraordinary proportions, and, in some animals, constitutes the greater portion of the cerebral hemisphere. In the anosmatics the hippocampal lobule is relatively small in those—such as in man and monkey—in which the sense of smell, though good, is subordinate to other sensory faculties; while in the balænidæ it is greatly reduced, and in the delphinidæ is almost entirely wanting. The posterior boundary of the hippocampal lobule is in the osmatics clearly indicated by an annectent gyrus, which interrupts the continuity of the limbic fissure and unites the lobule with the parieto-temporal part of the hemisphere. It is termed by Broca the *pli de passage rétro-limbique* (see Fig. 27, 9).

In man and the monkey the homologue of this gyrus is usually considered to be the pedunculus cunei, or cuneo-limbic annectent gyrus (see Fig. 28, *PCu*), connecting the cuneus with the hippocampal gyrus. Beauregard,[12] however, places it in the brain of the

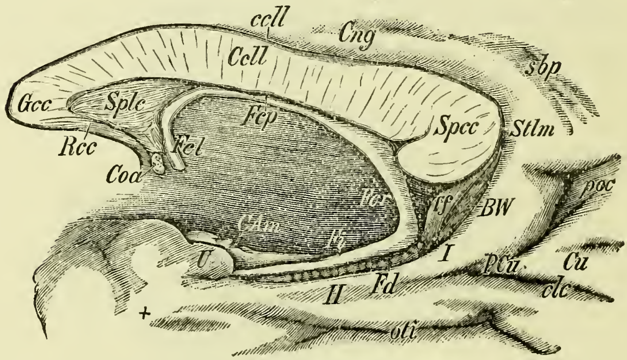

Fig. 28 (after Obersteiner).—*Ccll*, corpus callosum; *Gcc*, genu of corpus callosum; *Coa*, anterior commissure; *Fcl*, columns of fornix; *Fcr*, crus of fornix; *CAm*, cornu ammonis; *Tf*, tuberculum fascia dentatæ; *BW*, Balkenwindung (splenial convolution); *I*, isthmus gyri fornicati; *U*, uncus; *PCu*, pedunculus cunei; *Sbp*, sulcus subparietalis; *clc*, fissura calcarina; *Rcc*, rostrum of corpus callosum; *Spcc*, splenium of corpus callosum; *Splc*, septum lucidum; *Fcp*, body of fornix; *Fi*, fimbria; *Fd*, fascia dentata; *Stlm*, stria longitudinalis medialis; *g*, gyrus cinguli; *H*, gyrus hippocampi; *Cu*, cuneus; *ccll*, sulcus corporis callosi; *poc*, fissura parieto-occipitalis; *oti*, sulcus occipito-temporalis inferior.

whale at the extremity of the temporal lobe, immediately posterior to the uncus, and Zuckerkandl[13] assigns it a similar position in the brain of the dolphin.

I am inclined to think, on physiological grounds, that in man also and the monkey the posterior boundary of the hippocampal lobule is to be found in the annectent gyrus which connects the uncus with the anterior extremity of the temporo-sphenoidal lobe (+ Fig. 28). This is well seen in the brain of the chimpanzee which I show you. This would make the hippo-

[12] Sur l'Encéphale des Balænides.
[13] *Ueber das Riechcentrum*, 1887.

campal or pyriform lobule correspond with the gyrus uncinatus, and not with the gyrus hippocampi as a whole, which, as we have seen, is a portion of the tactile centre.

The relatively large size of the internal root in some animals, and its apparent connection with the anterior extremity of the gyrus fornicatus, led Broca to believe that there was a connection between the development of this region and the sense of smell; but the fact, which he himself admits, that the anterior portion of the callosal gyrus is particularly well developed in the brain of the Cetaceans, in which the sense of smell is merely rudimentary, is decidedly opposed to this hypothesis. Zuckerkandl, however, claims that the anterior extremity of the callosal gyrus in the dolphin is in some degree atrophied as compared with that of osmatic animals. The connection of the inner root with the callosal gyrus appears to me to be only superficial, and the probability is that this root really joins with the anterior extremity of what Zuckerkandl terms the marginal gyrus (*Randwindung*), which forms the callosal margin of the falciform lobe, and is continuous posteriorly with the fascia dentata (see Fig. 28, *Fd*). The dorsal or supracallosal portion of this gyrus is in anosmatic animals almost entirely obliterated, the atrophied remnants constituting the nerves of Lancisi (*Stlm*, Fig. 28), which are visible in man on the superior surface of the corpus callosum. He also describes, as peculiar to osmatic animals, a process of the falciform lobe which projects below the splenium of the corpus callosum, and which he terms the "*Balkenwindung*" (splenial gyrus.) Schwalbe, however, regards this merely as a portion of the gyrus dentatus. It is often seen in man (*B W*, Fig. 28). Zuckerkandl endeavours also to establish a relation between the development of the sense of smell and the size of the hippocampus or the cornu ammonis. He contends that in the dolphin the cornu ammonis is reduced to an insignificant remnant, and maintains, in opposition to other anatomists, that what has been regarded as the hippocampus, and which, topographically, and in its other relations, corresponds with this structure, is no hippocampus at all, but merely a prominence in the descending cornu of the lateral ventricle, corresponding to the eminentia collateralis of Meckel. Not having facilities for a proper investigation of this point, I requested the opinion of Sir W. Turner. He wrote me as follows:

"I will describe a dissection I have made of the descending horn of the lateral ventricle in the brain of a porpoise. This horn was continuous with the posterior end of the body of the

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lateral ventricle, and passed forwards and downwards into that lobe of the hemisphere which, from its position, may be called temporo-sphenoidal. It contained a well-defined eminence along its floor which was undoubtedly the hippocampus major. This eminence, 23 millimètres long, swelled out as a club-shaped end anteriorly, which was from 4 millimètres to 5 millimètres in transverse diameter.

Along the inner border of the hippocampus, the posterior pillar of the fornix was attached as the tænia hippocampi. The choroid plexus projected towards the descending horn immediately internal to the tænia hippocampi. The gyrus hippocampi lay in relation to the inner concave border of the tænia hippocampi; it was between 5 and 6 millimètres in breadth, and terminated anteriorly in a lobus hippocampi, the greatest breadth of which was 8 millimètres."

Sir W. Turner's dissection is, therefore, opposed to Zuckerkandl's view as to the absence of the hippocampus in the porpoise. Though the hippocampus is well developed in osmatic animals, it cannot be said to be atrophied in man and in the monkey, or to undergo variations in size with the other parts admittedly in relation with the olfactory tracts. It is questionable whether the hippocampus in man is relatively smaller than that of the lower animals; but, as to its absolute size, Sir W. Turner says: "Possibly the elephant, and it may be the largest whales, possess a hippocampus absolutely as large as that of the human brain, but I am inclined to think that the human hippocampus is absolutely larger than in mammals generally."

The hippocampal lobule, however, is relatively much smaller in man than in the osmatic animals, and perhaps is absolutely smaller than in many of them. What are the conditions which lead to variations in size of the hippocampus[14] cannot be said to be clear, but there appears to be an inverse ratio between the size of the gyrus fornicatus and gyrus hippocampi. This is so in the Cetaceans and Delphinidæ, in which the gyrus fornicatus is unusually large and more richly convoluted than in the higher animals. So, also, in the osmatic animals generally, the gyrus fornicatus is relatively larger than the gyrus hippocampi (apart from the hippocampal lobule). In the kangaroo the gyrus hippocampi and hippocampus merge with the gyrus fornicatus, and the hippocampus appears as the inrolled edge of this gyrus (see

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14 In my experiments on the hippocampal region, it was not possible to distinguish between lesions of the hippocampus apart from those of the gyrus hippocampi.

Fig. 29). This indicates a functional community between the hippocampus and the rest of the falciform lobe, which we have seen is related to the general sensibility of the body.

By means of the anterior commissure (olfactory division) the olfactory bulbs and tracts are connected with each other. This connection is best seen in those animals which have large olfactory bulbs (see Fig. 30, *po*), but a similar connection can also be traced in the brain of the monkey and the man (see Fig. 31, *ac*). The anterior commissure also connects the hippocampal lobules together (Fig. 30, *pt*). This division of the anterior commissure (temporal division) does not altogether vary in size with that of

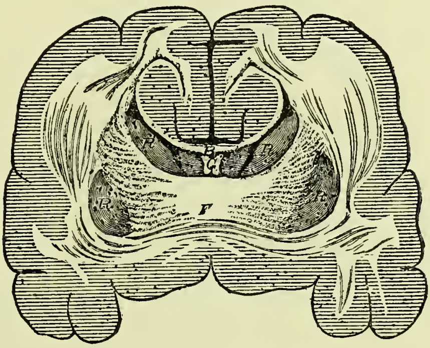

Fig. 29.—Frontal section of brain of kangaroo (Macropus major) (after Flower). *B*, body of corpus callosum (connecting the hippocampi, ; *F*, anterior commissure ; *G*, septal area ; *R*, corpus striatum.

the hippocampal lobule. It varies probably inversely with the corpus callosum, as Flower has pointed out.[15] Thus, in the dog, whose hippocampal lobule is seven times as large as that of the rabbit, the temporal division of the anterior commissure is a third smaller. The relative size of the olfactory and temporal divisions is opposed to the theory of Meynert that the anterior commissure forms a chiasma similar to the optic, where the olfactory tracts decussate with each other. And, further, it has been shown by the investigations of Ganser and von Gudden[16] that when one olfactory bulb is removed the whole of the olfactory division of the anterior commissure becomes atrophied on both sides, while the temporal division remains unaltered. We may, therefore,

[15] *Phil. Trans.*, 1865, On the Cerebral Commissures of the Marsupialia and Monotremata.

[16] *Archiv f. Psychiatrie*, Band 9.

assume that if the olfactory tract is related to the opposite hemisphere the path is not through the anterior commissure. Anatomically the olfactory tract appears to be in relation only with the hemisphere on the same side, but there are clinical facts which are difficult to explain otherwise than on the supposition that some at least of the fibres connecting the olfactory tract with the hemisphere pass into the internal capsule of the opposite side. By

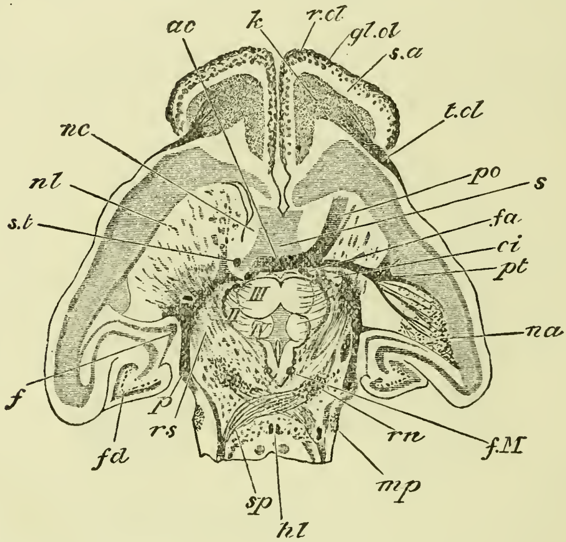

Fig. 30.—Horizontal section of the brain of the mole on a level with the anterior commissure (× 4) (after Ganser). *ac*, anterior commissure, dividing into *po*, pars olfactoria, and *pt*, pars temporalis; *ci*, internal capsule; *f*, fimbria; *fa*, anterior pillar of fornix; *fd*, fascia dentata; *fM*, Meynert's fasciculus; *gl. ol*, glomeruli olfactorii; *hl*, posterior longitudinal fasciculus; *k*, granular layer of olfactory bulb; *mp*, middle peduncle of cerebellum; *na*, nucleus amygdalæ; *nc*, nucleus caudatus; *nl*, nucleus lenticularis; *P*, pyramidal tract; *rn*, red nucleus; *r. ol*, roots of the olfactory nerve; *rs*, regio subthalamica; *s*, septum lucidum; *sa*, substantia alba; *sp*, superior cerebellar peduncles; *st*, stria terminalis; *t. ol*, tractus olfactorius.

means of the fornix the olfactory tract is brought indirectly in relation with the anterior tubercle of the optic thalamus, but there is no correspondence in size between the olfactory tract and the anterior pillar of the fornix. For, in the rabbit, the anterior pillars of the fornix are not more than one-third of the sectional area of the olfactory tract; and in man, while the olfactory tract is a mere thread, the anterior pillar of the fornix is 3 millimètres in diameter.

A certain portion of the fibres constituting the fornix are according to Owen [17] commissural fibres connecting the hippocampi with each other. This is seen very clearly in the brain of the kangaroo, in which, as above described, the hippocampus is an induplication of the gyrus fornicatus, the commissural fibres between the two constituting what is commonly called the corpus callosum in these animals. (*B*, Fig. 29). In man also the posterior part of the fornix consists of transverse fibres constituting the psalterium or lyra Davidis. The fact that the hippocampi are connected together by a distinct system of commissural fibres pleads also in favour of a functional differentiation of these structures from the

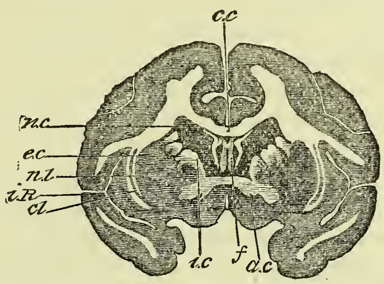

Fig. 31.—Frontal section of brain of monkey at right angles to the crura cerebri in the region of the anterior commissure (nat. size). *ac*, anterior commissure; *cc*, corpus callosum; *cl*, claustrum; *ec*, external capsule; *f*, pillars of fornix; *ic*, internal capsule; *iR*, island of Reil; *nc*, nucleus caudatus; *nl*, nucleus lenticularis.

hippocampal lobules, which are connected together by the posterior or temporal division of the anterior commissure.

The effects of electrical irritation of the hippocampal lobule in the monkey and other animals are such as may be most reasonably interpreted as being indicative of subjective olfactory sensation, namely, a peculiar torsion of the lip and nostril on the same side. Occasionally, however, the reaction is bilateral, and especially so in the rabbit. The reaction is that actually induced in these animals by the application of an irritant, such as a pungent odour, directly to the nostril. I have not observed any similar reaction on stimulation of the exposed hippocampus. But while we can be more or less certain, from the outward reactions, that subjective olfaction is aroused by stimulation, it is an exceedingly difficult problem to determine whether smell is lost by

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[17] *Comparative Anatomy of the Vertebrates.*

destruction of the same region. In some animals this is more easy than in others, and dogs, whose nose forms the chief organ of intellectual perception, would seem better adapted for experiments of this kind than monkeys. I have found it very difficult to determine the appreciation of odours by monkeys from any outword signs of like or dislike. To most, what we should consider very disagreeable odours mixed with their food they seem perfectly indifferent. I have tested them with sulphuretted hydrogen, bisulphide of carbon, valerian, assafœtida, iodoform, crotonchloral, and various other substances, but they have rarely refused their food on that account. The only odour which they seem uniformly to dislike—and that, perhaps, more from the associated taste than the smell itself—is aloes. I have rarely, if ever, found any monkey willing to eat fruits or other articles of food sprinkled with this drug. I have, therefore, almost exclusively used aloes to test both the smell and taste of these animals.

In my earlier experiments I found that in several instances in which I had primarily, or by secondary inflammation, cut off or disorganised the lower temporal regions on one or both sides, there were, for the time at least, indications of impairment or abolition of the reactions usually excited by pungent odours or disagreeable tastes. My experiments in this direction were, I admit, not very exact.

Schäfer and Sanger-Brown [18] have been unable to detect any indications of impairment or loss of the senses of smell and taste from destructive lesions of the lower extremity of the temporal lobes on both sides. They say, page 324, "Animals with the antero-inferior portion of the lobe, including the subiculum, completely cut away, smell their food, immediately detect a malodorous substance, such as aloes or assafœtida, with which it (that is, the raisin) may have been smeared, and cast it aside without tasting. A raisin into which quinine has been inserted is smelt, eagerly bitten, and immediately rejected with expressions of disgust." On looking at the figures which accompany their paper, however, I can see only one (No. 2, Plate 4) in which the anterior extremity appears to have been completely removed. In all the other portions of the hippocampal lobule are still to be seen on both sides.[19] In the notes referring to the experiment No. 2, I do not see any reference to tests of the animal's sense of smell, but it

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[18] *Phil. Trans.* B. 30. 1888.
[19] Figs. 1b, 3a, 6c., *op. cit.*

is stated that on the second day it gave clear indications of retaining its sense of taste unimpaired. But as to the others, sufficient I think is left of the hippocampal region on both sides to permit of the sense of smell being retained, even if not so acutely as before. I have, therefore, thought it desirable to make some new experiments in reference to this point.

I have in three monkeys removed the anterior portion of the temporal lobes by successive operations, but only one of the animals survived the double operation sufficiently long to allow of any satisfactory observations being made. In this case the anterior part of the left temporal lobe was practically entirely

Fig. 32.

removed, with the exception of a small fragment of the hippocampal lobule entirely detached from the rest (Fig. 32). In effecting the lesion the left optic tract was disorganised, and slight damage was also inflicted on the crus cerebri, so that the animal became completely hemiopic towards the right, which condition continued till death. There was also slight hemiplegia with hemianæsthesia on the right side, which, however, completely passed off in the course of a fortnight. The second lesion was established a month after the first. The removal, however, was not so complete, and it will be seen that the surface of the hippocampal lobule immediately adjoining the crus is still intact, though it is almost entirely undermined. The olfactory tracts were absolutely normal, as well as all the other cranial nerves and the rest of the brain. The animal was allowed to survive for three months, at the end of which time it was killed with chloroform. The cut surfaces of the temporal lobes were found firmly adherent to the middle fossæ of the skull, and the meshes of the adhesions were infiltrated with fluid; otherwise all had a normal appearance. The symptoms observable in this animal are of considerable interest.

Within a week after the establishment of the first lesion numerous observations were made in regard to the sense of smell and taste, which resulted in demonstrating that these were at least good. It was impossible to ascertain definitely whether there was any unilateral impairment, but they were as a whole keen enough to enable the animal to avoid and discard substances formerly distasteful to it. Thus, it refused to eat pieces of apple smeared with aloes, smelling them and at once throwing them down. A piece of apple sprinkled with sulphate of magnesia it examined carefully by smell, and, after tasting a mouthful, threw it away. It, however, eagerly devoured a piece which had not been in any way drugged. Similarly it refused to eat apple sprinkled with sulphate of zinc, and would not touch a piece smeared with colocynth. Such and similar observations were frequently made and confirmed, and there was no doubt whatever that it enjoyed excellent olfactory and gustatory sensibility.

On the day after the second operation, and for two days subsequently, the animal was in good physical health and strength, though somewhat dull, appeared to have lost all inclination to eat spontaneously, but it devoured greedily whatever was offered it, and showed no signs of disgust when pieces of food were given it copiously sprinkled with aloes; nor did it make any grimace when a pinch of aloes was placed in its mouth, but continued eating unconcernedly. On the fifth day after the operation the condition was still the same. On this day, while picking up its food from the floor of the cage, it not infrequently filled its mouth with sawdust, of the nature of which it did not seem to be aware. On the sixth, seventh, and eighth days similar tests were repeated with precisely the same results. There was no expression of disgust when the food offered it was copiously sprinkled with aloes, colocynth, or quinine. On the eleventh day a pinch of colocynth placed in its mouth caused no sign of distaste; the same placed in the mouth of its companion monkey caused violent nausea. On the eighteenth day the animal, which was very tame, would lick one's fingers which had been dipped in powdered aloes, and it drank up a dish of milk mixed with the same substance which its companions would not touch. A third animal which was offered the dish took a sip, and then, after a doubtful look, smacked its lips suspiciously, and would not take any more. In order to associate the disagreeable taste of aloes with a very definite and strong smell, I had some powdered aloes mixed with musk, so that there should be no doubt whatever as to the odoriferous character of the objectionable substance. This, however, made no difference. Pieces of food smeared with musk-aloes were eaten quite as readily as others; it seemed to have no suspicion of tricks played upon it, for it would come and lick musk-aloes off the blade of a knife as if it had been something nice. Its companion, however, looked askance and kept at a safe distance after having once experienced the result. At the end of a month the animal, which was in perfect health and full of fun and romps, continued unconcernedly to eat raisins smeared with musk-aloes, which its companion threw down at once as soon as it smelt them. Six weeks after the operation, a pinch of aloes was placed in its mouth. It seemed quite indifferent, and exhibited no signs of disgust. The same placed in the mouth of its companion caused retching, salivation, and comic attempts to rub the offending substance from its lips and tongue. Another animal which had not been tested in this way before vomited profusely several times, but our experimental animal within a few minutes afterwards did not refuse to lick some of the same powder off the blade of a knife. Two months after the operation it still did not refuse to lick a finger smeared with musk-aloes, and ate several pieces of apple smeared with the same, which none of the other animals, three in number, would have anything to do with. It also licked up a quantity of sugar, which was copiously mixed with aloes. The quantity of the drug it ate not unfrequently produced the usual medicinal effect. For nearly three months after the operation, the monkey continued almost entirely indifferent to substances, the smell and taste of which were such as to cause the other monkeys to avoid them, and made no grimaces when they were placed in its mouth. But it began at this time to show indications that it did not relish them, as it not unfrequently dropped pieces of apple and other morsels of food which were sprinkled as before. It occasionally sniffed at what was offered it before proceeding to eat, and would throw it down without tasting. But whether this was due to any sense of smell or merely an habitual action was not quite clear, for it would throw down shells of nuts, crusts of bread, and husks, which are practically without smell, after examining them. It also exhibited likes and dislikes in the matter of food, as, for instance, preferring apples to boiled potatoes, and it seemed to like sugar and boiled rice; but whether these likes and dislikes depended upon purely sapid characters I could not positively determine. The general results, however, of my observations incline me to believe that the animal's faculties of smell and taste, though obviously impaired, were not entirely abolished. It, however, for a considerable time after bilateral destruction of the lower extremity of the temporal lobe, did not refuse to eat substances the smell and taste of which are in the highest degree objectionable to normal animals, and I do not think it is possible to explain this otherwise than on the hypothesis that the centres of olfactory and gustatory perception were, if not completely, at least extensively disorganised. It would have been well to have carried out further observations on this point, but—owing to the rather excessive mortality among my monkeys occurring at the time of the influenza epidemic—I have not been able as yet to extend my researches in this direction.

An interesting accidental experiment on a dog has been recorded by Munk which is of importance in reference to the question before us. Munk observed that a dog which he had rendered blind by bilateral destruction of its visual centres seemed unable to discover by the sense of smell pieces of meat which were scattered before it. A slight sniffing which it occasionally made was the only indication that it might possess some traces of olfactory sensibility. The animal continued in this condition for several months, at the end of which time it was killed. It was found after death that the whole of the hippocampal gyrus on each side was converted into a thin walled transparent cyst, full of fluid. Except for the cicatrices caused by the removal of the occipital lobes, the brain was otherwise normal, as well as the olfactory tracts and bulbs. Though Munk is of opinion that this case shows that the hippocampal gyrus is the centre of smell, yet inasmuch as the hippocampal lobules were implicated as well as the rest of the hippocampal gyri, we may regard it as merely a confirmation of the facts which indicate that the sense of smell is localised more particularly in the hippocampal lobule.

Luciani,[20] as the result of his experiments on dogs, concludes that: "No evident deficiency of smell follows extirpation of the temporal lobe; but if the lesion extend to the neighbouring convolution above the fissure of Sylvius, one observes a notable diminution of that sense. Finally, a number of experiments show that an extensive decortication of the gyrus hippocampi, as well as partial ablation of the cornu ammonis, produces olfactory disorders, at first an almost complete loss of smell—a fact which seems to indicate to us that this portion of the brain is the central point of the olfactory sphere."

Luciani is also of opinion that each centre is in relation with both nostrils, but more particularly with the nostril on the same side. In the diagram, however, which he gives of the limits of the olfactory sphere, he extends it upwards into the parietal region as far as the longitudinal fissure, and partly, also, towards the frontal lobe. In regard to the sense of taste, he states that on one occasion, in a dog, he found that, after unilateral extirpation of the fourth external convolution, and of a portion of the gyrus hippocampi, the animal seemed to be less sensitive to bitters (digitaline) on the opposite side of the tongue. (This is misstated in *Brain*. A reference to the original experiment[21] shows that the lesion was in the left hemisphere; smell was lost in the left nostril, and taste on the right side of the tongue.)

Clinical and pathological evidence in favour of the localisation of the senses of smell and taste is as yet comparatively scanty. We have seen that, from anatomical considerations at least, the olfactory centre is in direct relationship with the nostril, but I have already mentioned that the symptoms of hysterical hemianæsthesia would appear to indicate that the olfactory, like the other centres of special sense, are in relation with the opposite side. It is questionable whether the coincident general anæsthesia of the nostril met with in this condition altogether explains the anosmia; for I have found that smell is not abolished when the general sensibility of the nostril is lost in consequence of disease of the fifth nerve. It is, however, difficult, with our present knowledge, to trace an anatomical connection between the nostril and the opposite side of the brain. The matter is, therefore, one which requires further investigation. There are clinical cases which plead in favour of the direct relationship of the olfactory centres. It may be objected against those reported by Ogle,

[20] "Sensorial Localisations in the Cortex Cerebri," *Brain*, 1885.

[21] *Die Functions-Localisation auf der Grosshirnrinde*, p. 117.

Fletcher and Ransome,[22] in which anosmia was found associated with aphasia and right hemiplegia, that there may have been direct implication of the olfactory tract or bulb. But a case has been reported by Churton and Griffith,[23] in which smell was impaired on the same side as the lesion, namely, a tumour which caused erosion of the uncinate convolution, and which did not appear to have, directly at least, affected the olfactory tract.

Several cases have been recorded of olfactory auræ or crude sensations of smell, in association with lesions implicating the region of the uncinate gyrus. One has been reported by McLane Hamilton,[24] without any implication of the olfactory nerves. Another has been recorded by Worcester,[25] and a third by Hughlings Jackson and Beevor,[26] in which the whole of the anterior end of the right temporo-sphenoidal lobe was the seat of a tumour involving the nucleus amygdalæ and the medullary fibres. Smell, however, was not lost in this case, either on the one side or on the other, which can be accounted for by the fact that the whole of the centre was not destroyed by the tumour.

This case as well as the others noted are, as Dr. Jackson remarks, of considerable value in determining sensory localisation, though naturally they do not afford such precise indications as to the position and limits of the centre as are afforded by destructive lesions causing entire abolition or considerable impairment. So far as they go, however, they harmonise with the results both of anatomical and physiological investigation. The smacking of the lips and tasting movements which are sometimes observed along with crude sensations of smell—"the dreamy states" of epileptic attacks—are probably discharges of the gustatory centres; but we have still fewer pathological facts bearing upon this point than on the situation of the olfactory centres. A case has been related by Dr. James Anderson[27] of a peculiar smell and taste sensation and dreamy state associated with tumour affecting the left temporo-sphenoidal lobe; but the lesion was too extensive, and too indefinite to allow of any precise conclusions being founded on it as to the position of the gustatory centre.

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[22] See *Functions of the Brain*, 2nd Edition, p. 321.
[23] *Brit. Med.* JOURNAL, May 28th, 1887.
[24] *New York Med. Journ.*, vol. xxxiv.
[25] *Amer. Journ. of Insanity*, July, 1887.
[26] *Brain*, October, 1889.
[27] *Brain*, vol. ix, 1887, p. 385.

LECTURE VI.

LECTURE VI.

Mr. President and Gentlemen,—I now come to the consideration of the physiological signification of the Rolandic area of the monkey and man, and its homologues in the brain of the lower mammals. I have already described with some detail the movements which are capable of being excited by electrical stimulation of the different regions included within this area. How these movements are to be interpreted is a subject on which there are great differences of opinion. The definite purposive character of the movements, however, their correspondence with the ordinary volitional activities of the animals, and, above all their uniformity and predictability, harmonise best, in my opinion, with the hypothesis that they are indications of the functional excitation of centres directly concerned in effecting volitional movements, and anatomically a part of the motor apparatus.

It has been established by experiments on monkeys—and now so generally admitted that it is almost unnecessary to enter into detailed proof—that destruction of the centres, excitation of which produces definite movements causes paralysis (*quâ* volition) of the same movements on the opposite side of the body, varying in degree, completeness, and duration with the extent of the destruction of the respective centres. When the destruction is complete the paralysis is permanent, and is followed in due course by descending degeneration of the pyramidal tracts of the spinal cord, and secondary contracture in the paralysed limbs. As an illustration I quote the following experiment on a monkey which was exhibited at the International Medical Congress in London, 1881, eight months after the operation.

The cortex was destroyed as shown in the figure (Fig. 33), in the left hemisphere over an area embracing the ascending frontal and ascending parietal convolutions, except at their upper and lower extremities. The lesion also invaded the base of the superior frontal convolution, and the anterior limb of the angular gyrus. There was thus destroyed nearly the whole of the motor area on the convex aspect of the hemisphere, the centres for the leg, foot, and trunk being only partially destroyed; those for the angle of the mouth and tongue almost entirely escaping. The result of this lesion was almost complete right hemiplegia with conjugate deviation of the head and eyes to the left side. As in similar cases in man, the deviation of the head and eyes was only of comparatively short duration, and the partial facial paralysis, at first perceptible, also disappeared within a fortnight; but the paralysed condition of the limbs continued very marked. With the exception of slight power of flexion of the thigh and leg, the right lower extremity was helpless, and the right arm

Fig. 33.

was incapable of independent volitional movements. Occasionally, when the animal struggled, associated movements were observed in the right hand, similar to those initiated by the left, but only under such circumstances. The power of prehension was entirely annihilated. Cutaneous sensibility was unimpaired throughout. The slightest touch excited attention; and a pinch, or other painful stimulus, caused signs of sensation quite as vigorous as on the other side. This was the condition in which the animal was when exhibited at the International Medical Congress, and at this time well-marked contracture had become established in the paralysed limbs, with exaggeration of the tendon reactions, as in cases of incurable cerebral hemiplegia in man.

The investigation of the brain of this animal was carried out by a committee appointed by the Physiological Section, and the position of the lesion in the motor zone, and its limitation to the cortex and subjacent fibres, were definitely proved by them. Microscopical investigation also demonstrated the existence of secondary degeneration in the pyramidal tracts of the right side of the spinal cord as far as the lumbar region.

In the case represented in Fig. 34 the lesion, which was established at the upper extremity of the fissure of Rolando in the left hemisphere, caused paralysis of the right leg, without affection of sensation, followed in due course by contracture of the paralysed

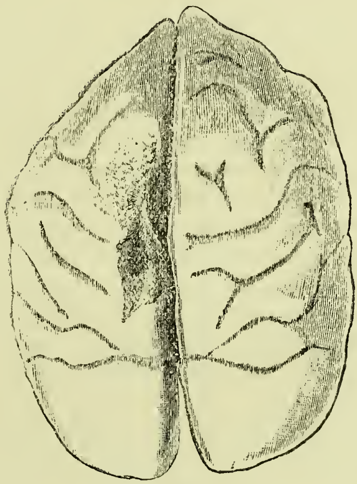

Fig. 34.

muscles. This condition remained unchanged for eight months, at the end of which time the animal was killed. In this case also secondary degeneration was demonstrated in the medullary fibres of the corona radiata, and in the pyramidal tracts of the opposite side of the spinal cord as far as the lumbar region, whence emerge the motor nerves of the lower extremity.

In another experiment the cortex was destroyed in the middle of the ascending parietal convolution and adjacent margin of the ascending frontal convolution of the right hemisphere. The result of this was almost complete paralysis of the left hand, and great weakness of the flexor power of the forearm. The shoulder movements, however, were unimpaired; the animal could stretch its arm forward, but could not grip with its hand what it wished to lay hold of. Tactile sensibility was absolutely unimpaired in the paralysed limb, the slightest touch on it at once exciting the animal's attention, and a painful stimulus, such as a pinch or touch with a heated wire, caused as lively signs of sensation as on the other side. This condition remained essentially unchanged for the two months which the animal survived the operation.

Many similar experiments have been recorded by Horsley and Schäfer,[1] and their observations on the functions of the marginal gyrus deserve special note. Extirpation of the marginal convolution causes paralysis of those movements which remain more or less unaffected after the destruction of the centres on the convex aspect of the hemisphere; namely, movements of the trunk, those of the hip muscles, as well as some of those of the leg. In order, however, that these movements should be entirely paralysed, it is necessary that the marginal convolution should be destroyed in both hemispheres; as it would seem that the trunk movements are so bilaterally co-ordinated in the marginal convolution, that the removal of one only is not sufficient to cause any very marked effect. When both are removed, however, the most absolute paralysis of the trunk muscles is induced. "The attitude and general appearance of a monkey in which this double lesion has been produced are very striking. Instead of sitting up with back somewhat curved, in the manner normal to monkeys, an animal which has been submitted to this operation lies prone, with legs and feet outstretched (or, at most, with flexed hips), back flat, tail straight and motionless, and arms put forward to clutch at any neighbouring object. The head retains its power of rotation, as well as flexion and extension, and the movements of the eyes and facial muscles appear normal. The animal frequently props itself upon its elbows, but never assumes the normal sitting attitude. If the monkey desires to sit up, it can only do so by dragging itself into the sitting posture by its arms and hands, and holding on by these to the wires of the cage, or to any neighbouring object. If the hold should be detached the animal immediately tends to fall over. Progression is effected almost entirely by the arms, the monkey dragging itself along with the aid of these, assisted by the flexion which occurs at the hips; the legs are quite limp and draggled, the dorsal surface of the toes being drawn over the ground."[2]

[1] *Phil. Trans.*, B. 20. 1888.
[2] See illustration, Fig. 20, *op. cit.*

Besides the movements of the trunk, there are others which are also bilaterally represented in each cerebral hemisphere. This holds in respect to the upper facial region, as well as those of the larynx. Hence, unilateral extirpation of the centres of these movements causes no, or scarcely any, perceptible impairment; and it is necessary that the centres should be destroyed on both sides in order that paralysis should result. It has been shown by Krause in dogs, and by Horsley and Semon in monkeys, that unilateral extirpation of the laryngeal centres does not appreciably impair the adduction of the vocal cords, whereas phonation becomes volitionally impossible when the centres are destroyed in both hemispheres.

It would appear from the researches of Franck and Pitres,[3] Exner,[4] Lewaschew,[5] Sherrington,[6] that such movements as are not primarily bilaterally represented in each cerebral hemisphere are secondarily associated, in accordance with a hypothesis originally advanced by Broadbent, by commissural fibres connecting the bulbar and spinal nuclei with each other. Though moderate stimulation of the cortical centres of the limbs gives rise to movements as a rule only on the opposite side, yet it not infrequently happens, if the stimulation be increased, that movements occur in the limbs on both sides. These are, however, more pronounced on the opposite than on the same side. In the monkey as well as in man, it is not unusual to find descending degeneration in both lateral columns as the result of unilateral cortical lesions.

According to the recent researches of Sherrington, if the cortical lesions affect only the centres for the limbs, bilateral degeneration does not occur, to any extent at least; but this is very pronounced if the lesions affect the marginal convolution. The degeneration is confined to the pyramidal tracts on the same side as far as the decussation of the pyramids, but becomes bilateral in the spinal cord. In the case, however, of the more obviously bilateral laryngeal centre, degeneration is well marked in the pyramids of both sides. These facts, as well as clinical observations in man, show that, even in the case of the limbs, each hemisphere represents both sides of the body, mainly the opposite, but to some extent also the same side.

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[3] *Leçons sur les Fonctions Motrices du Cerveau*, 1887.

[4] *Sitzungsb. d. Wiener Akad*, 3 Abth., pp. 185-190, 1881.

[5] *Archiv f. Physiologie*. Bd. 36.

[6] *Journ. of Physiology*, Nos. 4, 5, and 6; and BRIT. MED. JOURNAL, January 4th, 1890.

It was first pointed out by Brown-Séquard, and his observations have been confirmed by Pitres[7] and Friedländer,[8] that lesions which induce hemiplegia of the opposite side also cause some diminution in the energy of the movements of the limbs on the same side. This is a result which we should expect if each hemisphere were in relations with both sides of the body.

The bilateral relations of each hemisphere, which exist to some extent in monkeys and man, are, as we shall see, still more pronounced in the case of dogs and the lower animals; and, in dogs, as Sherrington has shown, bilateral degeneration from unilateral cortical lesion is more commonly met with. This bilateral representation accounts for a certain amount of recovery, even when the motor centres of one hemisphere have been entirely destroyed; and this recovery extends more particularly to those movements of the limbs which are more or less habitually associated with those of the other side, and least of all to those which are more independent and more volitional. Hence, in cortical paralysis, the arm is more paralysed than the leg, and the distal movements of the arm more than the proximal, These facts are of great importance in reference to the hypothesis of the functional compensation for the centres which have been destroyed by neighbouring, or other, portions of the same cerebral hemisphere. It has now been established beyond all question that cortical lesions of the motor zone in man, if they are such as actually to destroy and not merely push aside the grey matter of the respective centres, invariably cause paralysis of volitional motion in the related parts. Such results have invariably followed, not only the destructive lesions of disease but also surgical excisions of the cortical centres. Not only does general hemiplegia result from lesions of the whole of the Rolandic area, but limited lesions cause limited paralyses, or monoplegiæ, of the face, arm, and leg, in precise correspondence with the results of experiments on monkeys.

In the Gulstonian lectures on Localisation of Cerebral Disease, which I had the honour of delivering in this College twelve years ago, I brought before you a number of cases, collected from various sources, in support of these statements. Since then many others have been recorded, all confirming the same; and the point has now been considered so completely proved, that clinical observers have practically ceased to record their observations.

Of 483 cases of cortical (including subcortical) disease collected

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[7] *Archives de Neurologie*, No. 10, 1882.
[8] *Neurologisches Centralblatt*, No. 11, 1883.

under my direction by Dr. Ewens (excluding as a rule tumours and other lesions likely to cause indirect affection of other parts), I have the records of 110 cases of hemiplegia of the opposite side from general lesion of the Rolandic zone; and 90 cases of monoplegia from limited lesions of this zone. Of these, 11 are cases of crural monoplegia, from disease of the paracentral lobule; 15, cases of paralysis of the arm and leg from disease of the paracentral lobule and upper third of the ascending convolutions; 33, cases of brachial monoplegia, including three cases of surgical excision, from lesion of the middle of the ascending convolutions; 19, cases of paralysis of the arm and face from lesions of the lower half of the Rolandic zone; and 10, cases of facial paralysis from disease of the lower third of this region. In addition to these, I have notes of 20 cases of atrophy of the cortex of the Rolandic zone in connection with congenital or infantile hemiplegia, or as the result of congenital absence, or long-standing amputation, of a limb.

In the monkey and man, therefore, there is no evidence of functional compensation for the paralysing lesions, except in so far as these may be accounted for by the bilateral relations of each cerebral hemisphere. The theory of compensation by other portions of the same hemisphere has been adduced more particularly in order to account for the apparent recovery in dogs and lower animals after complete unilateral destruction of the cortical motor centres. This is a hypothesis, however, which is inconsistent with the principles of localisation otherwise maintained by those who advance it; and for which, moreover, there is no necessity. Though dogs appear to recover from the disorders of movement, which are at first obvious enough after unilateral extirpation of their motor centres, yet, in reality, the recovery is never complete. Only those movements are permanently affected which are the least automatic and most volitional; while those which are most automatic and least volitional, such as those concerned in station and co-ordinated locomotion, and which, as we have seen in the first lecture, may continue in some animals even after complete extirpation of both hemispheres, are comparatively little impaired. The movements which are most paralysed are those of the limb, as a hand, or organ of prehension.

It appeared from Goltz's earlier experiments on dogs that the use of the forelimb as a hand, such as in giving a paw, holding a bone when gnawing it, etc., was permanently paralysed by destruction of the motor centres of the opposite hemisphere. But in his last interesting communication[9] he has shown that this is not strictly correct. He gives the particulars of a dog in which practically the whole of the left hemisphere was destroyed, and which lived fifteen months afterwards. In this animal, the movements of the right limbs, so far as station and locomotion were concerned, were so little affected, though not really normal, that the defect might readily escape superficial observation altogether. It had not entirely lost the use of the right paw as a hand in holding a bone, at least in association with the left, though in this respect it was very imperfect. This animal had not been taught to "give a paw," so that it could not be determined whether this acquired trick could still be exhibited, though Goltz is of opinion that, in rare cases, a dog may perform this act after deep and extensive (but probably not complete) destruction of the motor zone of the opposite hemisphere. The possibility of a certain degree of independent, or rather associated, volitional use of the opposite limbs is, as Goltz's experiments clearly demonstrate, dependent on the integrity of the motor centres of the uninjured hemisphere; for when these are destroyed on both sides, all strictly volitional movements are permanently paralysed. Thus he says; "A dog whose motor centres of both hemispheres have been destroyed cannot feed itself; the movements of the tongue are greatly impaired, while the tongue, in a case of unilateral extirpation, can be moved normally. The animal can, as already mentioned, still walk, but in a very awkward and unsteady manner. All movements of the paws as hands appear to be utterly impossible."[10] This powerlessness depends on the symmetrical destruction of the motor centres in both hemispheres; for, if the motor centres on the one side, and the occipital regions on the other, are destroyed, the dog can eat and drink and move its tongue, walk and run about fairly well, and use both its forepaws, to some extent, in fixing a bone which it is gnawing. What is true of the bilateral representation of the motor faculties in each cerebral hemisphere appears also to hold in respect to the faculties of general and special sense.

Apart from motor paralysis, I have never been able to detect the slightest impairment of special, or tactile and general sensibility after destruction of the motor centres. One may observe absence or defective reaction of, the paralysed limbs to sensory stimulation; but that this is not dependent on defective sen-

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[9] *Archiv f. Physiologie*, vol. xlii, 1888.

[10] *Op. cit.*, p. 448.

sation is shown by the fact that the animal's attention is at once attracted by the slightest touch on the paralysed side, and by general signs of discomfort if any part is subjected to painful stimulation, such as the prick of a pin. The contrast between the reactions to sensory stimulation in monkeys, in which the falciform lobe, and those in which the motor centres have been removed, is so striking that no doubt can be entertained that, in the latter case, sensibility is retained, while, in the other, it is abolished or profoundly impaired. Horsley and Schäfer have also been unable to obtain any evidence of loss of general sensibility after destruction of the motor centres.

"We have seen," say they, "sufficient, however, to convince ourselves that a lesion of the cortex which produces paralysis of volitional motion in a part, is not necessarily accompanied, also, by loss of general sensibility of the paralysed part."[11] In order to test the hypothesis which has been advanced by some—that the superficial cells of the motor cortex are sensory in function—they, in one instance, destroyed the superficial layers of the grey matter by means of the actual cautery. "In spite, however, of the complete blocking of the superficial vessels so produced," they go on to say, "we obtained only an incomplete muscular paralysis as the immediate result of the operation; but although the superficial layers of the cortex must have been destroyed, there was no diminution of sensibility in the parts affected by paresis. The subsequent softening and disintegration which occurred in consequence of the thromboses caused by the cautery was accompanied by a much more complete condition of muscular paralysis; but the general sensibility of the opposite side was still apparently unaffected, and continued so until the death of the animal."[12] One of Goltz's experiments on dogs[13] also showed very clearly that destruction of the cortical motor zone does not impair sensibility on the opposite side. Taking advantage of the well-known fact that dogs snarl when touched while engaged in eating, he touched the right side of a dog so occupied, which had had its motor centres in the left hemisphere destroyed some time previously. The animal responded invariably with the characteristic signs of displeasure on the slightest touch. Similar facts have been demonstrated in the case of cats by Bechterew.[14] "It is a familiar obser-

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[11] *Op. cit.*, p. 15.
[12] *Op. cit*, p. 17.
[13] *Pflüger's Archiv*, Bd. 34, 1884, p. 465.
[14] *Pflüger's Archiv*, Bd. 35, 1885, p. 137.

vation that a cat dislikes having its feet wet, so that, if it should accidentally step on a wet place, it will stop and shake its paw dry before proceeding further; or if, while indolently slumbering, a drop of water falls on it, it will start up and make off hastily; or it will close its eyes and contract its ears if its paw is gently touched unobserved." After verifying these facts in a cat about to be operated upon, Bechterew removed the cortex in the region of the sigmoid gyrus. On recovery from the chloroform narcosis the animal exhibited the characteristic motor disorders of the right limbs, and was unable to use the right paw for any independent volitional act, but touching the ear, or the sole of the right as well as the left foot, induced the same closure of the eyes, and drawing in of the ears as before; and the sprinkling of a few drops of water on its paralysed side caused the animal to start up and make off as before.

It has, however, been maintained by various experimenters, Hitzig, Nothnagel, Schiff, Munk, Tripier, Goltz, Luciani, etc., that the affection caused by destruction of the so-called motor centres is accompanied by, or dependent on, affections of tactile, muscular, or general sensibility, or all three combined, in the paralysed limbs.

My own experiments, as well as those of Horsley and Schäfer, have shown that there is no discoverable impairment or loss of tactile or general sensibility after lesions of the motor zone, and I will not therefore stay to examine in detail the data, so far as they have been given, on which the various authors whom I have mentioned found their conclusions. They appear to me to be based merely on defective reaction to sensory stimulation, which can be equally well explained on the theory of motor inability as sensory deficiency; or they are due to the destruction of other regions than the motor cortex. This applies more particularly to the experiments of Goltz, in which the lesions of the hemisphere, or hemispheres, have been vague and indeterminate. It is unquestionable also that in man paralysis from lesion of the motor area is, in the majority of instances, an essentially motor affection, and is unaccompanied by any discoverable defect of tactile, muscular, or general sensibility. I have myself recorded several, and have collected many other cases of lesion of the cortical motor zone accompanied by paralysis, in which every variety of sensibility has been carefully tested and found normal. But it is true also that in a good many instances of lesion of the motor area some degree of impairment of tactile and muscular sensibility general or limited, has been observed. And several authors, Petrina,[15] Exner,[16] Luciani and Seppili,[17] Starr,[18] Dana,[19] Lisso,[20] have endeavoured to show, from examination of the clinical records of cerebral disease, that the motor centres and the centres of tactile and general sensibility coincide so that sensory disturbances, frequently at least, if not always accompany the motor paralysis. The data on which these conclusions have been based appear to me in the highest degree unsatisfactory. The lesions have been microscopical specks of themselves insufficient to cause anything; or, and for the most part, tumours which may cause everything; or multiple foci of disease not limited to the cortex itself. Causation is not established unless invariable and unconditional relationship has been shown to exist between a particular lesion and a particular symptom. In the case of the motor area it has been satisfactorily demonstrated that destructive lesions invariably give rise to motor paralysis, local or general, according to the position and extent of the lesion. A single case, therefore, of paralysis from lesion of the cortical motor area, unaccompanied by any defect of sensibility, is sufficient to overthrow a host of positive instances in which the two symptoms have apparently been caused by the same lesion. Apart, however, from all other considerations, an examination of the clinical records taken indiscriminately from all sources, excluding tumours and such lesions as are obviously calculated to cause widespread and indeterminate disturbances of other parts, is certainly not in favour of the conclusions which the above-mentioned authors have founded on this kind of evidence. For, of 110 cases of general lesion of the Rolandic zone causing hemiplegia, in 52 cases sensibility was unimpaired (in one of these a large portion of the motor cortex was excised).[21] In 37 the condition as to sensibility is not mentioned, while in 21 it is said to have been to some extent affected. But of these last, in one sensibility is stated to have been blunted over the little finger.[22] In another there was general hyperæsthesia, more marked on the paralysed side. In

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[15] Sensibilitätsstörungen bei Hirnrindenläsionen, *Zeitsch. f. Heilkunde*, Bd. ii, p. 375, 1881.

[16] *Localisation der Functionen in der Grosshirnrinde des Menschen*, 1881.

[17] *Die Functions-Localisation auf der Grosshirnrinde*, 1886.

[18] Localised Cerebral Disease, *Amer. Jour. Med. Sc.*, 1884.

[19] *Cortical Localisation of Cutaneous Sensations*, 1888.

[20] *Zur Lehre von der Localisation des Gefühls in der Grosshirnrinde*, 1882.

[21] Case of J. H., *Brain*, vol. x, p. 95.

[22] Tripier, *Rev. Mens.*, 1880, Case 4.

one all varieties of sensibility were retained, but the localisation of touch was somewhat defective.[23] In this case, however, the inner table of the skull had been driven into the brain substance, causing general hemiplegia.

In two the lesion extended deeply into the white substance. In one case the cortical lesion was complicated by the presence of a large tumour in the centrum ovale.[24] In one sensibility is said to have been blunted on both sides of the body. In another [25] the lesion was a large hæmorrhagic cyst in both central convolutions In this, and in five others, the island of Reil or external capsule was involved. In one hemiplegia was accompanied by anæsthetic formication of the paralysed foot. In this case there was tubercular deposit implicating the gyrus fornicatus as well as the central convolutions. In seven others there was diffuse meningo-encephalitis or tubercular meningitis.

In ten cases of crural monoplegia, from disease of the paracentral lobule, cutaneous sensibility was unaffected in six, its condition not mentioned in two, and affected in two. In the one[26] sensibility to pain was a little diminished in the paralysed limb, but this disappeared the next day. In the other[27] the leg became gangrenous, a condition which was preceded by anæsthesia.

Of fifteen cases of paralysis of the arm and leg from disease of the paracentral lobule and upper third of the ascending convolutions, sensation was intact in six, not mentioned in five, and affected in four others. In three of these the paracentral lobule was deeply involved, one of them being a tubercular mass ; and in only one was the anæsthesia marked or permanent. In all four the lesion was in immediate proximity to, or actually involved, the gyrus fornicatus. In one case, under my own care,[28] of traumatic cicatrix at the upper third of the ascending frontal convolution, excision of the lesion was followed by loss of tactile sensibility on the dorsum of the two distal phalanges, and inability to indicate the position of the fingers of this hand. This impairment of sensibility ultimately disappeared, while the motor paralysis continued as at first. In this case the lesion was such as to actually implicate the gyrus fornicatus.

Of 35 instances of brachial monoplegia, 5 were cases of excision

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[23] Bramwell's Case, BRIT. MED. JOURNAL, August 28th, 1875.
[24] Seguin's case, *Trans. Amer. Neurol. Assoc.*, 1877, p. 115.
[25] Starr's case, 75, *Amer. Journ. Med. Sciences*, July, 1884.
[26] Gouguenheim, *Soc. Méd. des Hôpitaux*, 1878, p. 48.
[27] Ballet, *Archives de Neurologie*, Tome v, p. 281.
[28] Case of J.B., *Brain*, vol. x., p. 26.

of portions of the cortex for the cure of focal epilepsy. In two, cases by von Bergmann[29] and Keen,[30] sensation was intact. In another case reported by Keen,[31] of hemiplegia and epilepsy, resulting from depressed fracture, there was, after the operation, slight impairment of sensation in the middle of the forearm and two inner fingers. But this condition of sensibility was similar to what had existed before the operation. In another[32] there was no obvious impairment in tactile (?) or muscular sensibility. The patient could not distinguish the form of objects owing to the inability to move his fingers. In a fifth case[33] the removal of a tumour from the right lower parietal region, which was the cause of epilepsy beginning in the thumb, was followed by tactile anæsthesia of the whole of the left side, together with loss of so-called muscular sense in the left arm. In this case the sensory tracts for the whole of the opposite side of the body were obviously implicated. Of the 30 others, sensibility was unimpaired in 12, not mentioned in 15, and affected in 3. In one of these the lesion was a gumma.[34] In the second[35] there was a clot compressing the island of Reil; in the third sensibility was said to have been extinguished over the entire surface of the body.[36]

Of 19 cases of lesion of the lower half of the Rolandic zone, causing paralysis of the face and arm, sensation was unaffected in 11, not mentioned in 5, and affected in 3. In one of these,[37] however, a blood clot in the island of Reil compressed the subjacent convolutions. In another reported by the same author[38] a small tubercle the size of a hemp seed, situated in Broca's convolution, is described as having caused (!) paralysis of the right side of the face and arm, and anæsthesia of the right side of the trunk. The third, also reported by Petrina, was similar to the second. In 10 cases of disease of the lower third of the Rolandic zone, causing simple facial paralysis, sensation was intact in 4, not mentioned in 5, and affected in 1. In this case[39] there was said to have been anæsthesia, not only of the face, but of half the trunk.

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29 *Archiv. f. Klin. Chirurg.*, p. 864, 1887.
30 *Amer. Journ. Med. Sc.*, 1888, Case 3.
31 *Ibid*, Case 2.
32 Lloyd and Deaver's case, *Amer. Journ. Med. Sc.*, 1888, p. 477.
33 Jackson and Horsley, *Brain*, vol. x, p. 93.
34 Martin, *Chicago Med. Jour.*, vol. 46, p. 21.
35 Wood, *Phil. Med. Times*, vol. v, p. 470.
36 Ringrose Atkins, BRIT. MED. JOURNAL, 1878.
37 Petrina, *Zeitsch. f. Heilkunde*, vol. xi, 1881, Case 1.
38 *Ibid.* Case 6.
39 Petrina, *sup. cit.*, Case 3.

It thus appears that, of 284 cases of lesion affecting the Rolandic zone, general or in part, in 100 the condition of sensibility was not mentioned; in 121 it was stated, and by many of the most reliable clinical observers, to have been intact; and in many of these[40] all varieties of sensibility are expressly stated to have been carefully investigated. In the remaining cases no detailed notes are given as to the different modes of sensibility, and the methods applied for testing them. In 63, some impairment of sensibility was noted. In 28 of these, the lesion was not confined to the Rolandic zone, but implicated adjacent lobes, especially the parietal. The remaining 35 have already been analysed, and it has been shown that, in the majority at least, conditions existed which were calculated to implicate either the sensory centres in the gyrus fornicatus, or the sensory tracts of the internal capsule. Even where these cannot have been demonstrated to exist—and I freely admit that there are such cases—it is more logical to assume that they may have existed than that in some individuals the tactile and motor centres should coincide, while in other this should not be the case. I do not consider that the sensory aura which occasionally precedes or accompanies a localised epileptiform spasm can be taken as a proof that the motor and sensory areas coincide. It may prove contiguity, functional or anatomical, but not coincidence. For the most careful investigation in a large number of cases has failed to detect the slightest impairment of any of the forms of general sensibility, while the motor affection has been of the most pronounced character. There is also no relation between the degree of affection of sensibility and that of the motor paralysis. The motor paralysis has been absolute

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[40] Mills (*Trans Amer. Cong. of Phys.*, etc., 1888, p. 269), (digest in *Brain*, October, 1889); Delépine (*Trans. Path. Soc.*, 1889); Ferrier (*Brain*, April, 1883, p. 67); Moutard-Martin (*Bull. Soc. Anat.*, 1876, p. 706); Laquer (*Inaug. Dissert. Breslau*, p. 91, Case 10); Mills (*University Med. Mag.*, November, 1889); Ferrier (*Brain*, vol. x, p. 95); Raymond et Derignac (*Gaz. Méd.*, 1882, p. 665); Von Bergmann (*Archiv. für klin. Chir.*, 1887, p. 864); Davy and Bennett (*Brain*, vol. ix, p. 74); Ballet (*Archives de Neurol.*, vol. v, p. 275, Case 1); Lloyd and Deaver, *Amer. Jour. Med. Sciences*, vol. 96, p. 477); Keen (Cerebral Surgery, *Amer. Jour. Med. Sciences*, 1888, Case 3). One might add to these cases not a few of hemiplegia with aphasia (not followed by *post-mortem* examination) in which the symptoms pointed to cortical lesion. In one, recently under my care at King's College Hospital, of absolute paralysis of the right arm associated with word-blindness and word-deafness, the patient was aware of the slightest touch on the paralysed hand, or of a drop of warm or cold water falling on it, and with eyes blindfolded could put her left hand on the spot, in whichever position her paralysed arm was placed. This is a method of testing the sense of position in those who are unable to understand or speak, and is also applicable to the lower animals.

while the affection of sensibility has been slight, and confined to one, or at most two or three, fingers; or the motor paralysis has been limited, while the impairment of tactile sensibility has been general. And in others the affection of tactile sensibility, at first observed, has disappeared, while the motor paralysis has remained. And when, moreover, we take into consideration the fact that tactile and muscular sensibility may be abolished in the absence of motor paralysis, a condition which can be experimentally produced in monkeys by lesions of the falciform lobe, we have a further proof that the motor and sensory centres of the cortex are anatomically distinct from each other, and that we cannot attribute the motor paralysis to any defect in tactile or muscular sense. The occurrence of slight defects in tactile and muscular sensibility, more particularly in the fingers, which have been noted by several as a special characteristic of lesions of the cortical motor zone, are, in my opinion, to be looked upon as the beginning or remnants of a general hemianæsthesia, rather than as indicative of special centres for the tactile and muscular sensibility of the digits in the motor cortex.

In illustration of this, I would mention the details of the following case. The patient was a lady, aged 50, suffering from word-blindness and a slight degree of right hemiopia, which, from these and other symptoms, I diagnosed to be due to a tumour in the region of the angular gyrus. There was no paralysis of motion, but there was slight impairment of the localisation of touch and the sense of position in the fingers of the right hand, the face and leg being normal in this respect. An operation was undertaken by Mr. Horsley for the removal of the tumour, but it was found, on trephining to be situated beneath the angular gyrus, and could not safely be removed. This was a case in which, without doubt, the sensory tracts of the internal capsule were implicated, but only to a slight extent; hence the limitation of the anæsthesia to the fingers. Had the implication of the internal capsule been more extensive, there would undoubtedly have been loss of tactile and muscular sensibility on the whole of the opposite side of the body.

This case has an important bearing on the hypothesis advanced, among others, by Nothnagel[41] that the centres of the muscular sense are situated in the parietal lobe. Defects of tactile sensibility, and of the sense of position of the limbs, have not infre-

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[41] VI Congress für innere Medicin. *Neurolog. Centralblatt*, 1887, vol. 6, p. 213.

quently been observed in connection with lesions of this region, sometimes complicated with hemiopia when the lesions have invaded also the occipito-angular region, as in the above case, and in one reported by Westphal.[42] But the real cause of these symptoms I believe to be implication of the sensory tracts of the internal capsule which lie underneath this region, and not affection of the cortex itself; for lesions of the inferior parietal lobe do not, in my experience, produce the slightest affection of general sensibility on the opposite side of the body.

Cortical lesions of the motor zone causing complete paralysis may occur without any impairment whatever of the muscular sense; and loss of the muscular sense may occur without motor paralysis. I agree with Bastian, James,[43] and others—and have furnished experimental proof thereof—who hold, in opposition to the views maintained by Bain, Wundt, and Hughlings Jackson, that the sense of movement, its range and direction, are dependent upon in-going, or centripetal, impressions conditioned by the movement itself, and not on the out-going current or energising of the motor centres.

We have, I believe, no sense of innervation independently of the sensory impressions arising from the parts which are moved. The energising of the motor centres and motor apparatus is revealed in consciousness only through the functioning of the correlated sensory tracts and centres. The idea or conception of a movement is, therefore, a revival in the respective sensory centres of the various impressions which have been associated with this particular movement. Of these the most important are the visual factors and those which are included generally under the so-called muscular sense. In learning a movement our chief guide is vision, which enables us to place our limbs in the position requisite to produce any desired effect, and we associate also with the particular movement a distinct set of muscular sense impressions. The revival of these, singly or conjointly, is the idea of the movement, and this allowed to excite the appropriate muscular combination is the volitional act itself.

I hold that the centres of the sensations which accompany muscular action, and which form in part the basis of our ideas of movement, are distinct from the cortical centres, through and by which the particular movements are effected. The destruc-

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[42] Zur Localisation der Hemianopsie und des Muskelgefühls beim Menschen, *Charité-Annalen*, 1882.

[43] *The Feeling of Effort*, 1880.

tion of the cortical motor centres paralyses the power of execution, but not the ideal conception of the movement itself. A dog with its cortical centres destroyed has a distinct notion of the movements desired when asked to give a paw, but it makes only ineffectual struggles and fails to comply. So, too, it not infrequently happens that a patient rendered hemiplegic by embolism of his Sylvian artery only discovers his infirmity by his inability to execute the movements which he has distinctly conceived.

Voluntary movements are capable of being carried out in the entire absence of all sense of movement. In the well-known case described by Schüppel,[44] the patient, anæsthetic from spinal disease, was able to co-ordinate his limbs perfectly, and move them freely and forcibly with the aid of vision; and even without the aid of vision to employ them with a fair degree of precision and steadiness. A similar condition is met with in hemianæsthesia from organic lesion of the sensory tracts of the internal capsule, and in the functional forms described under the name of hysterical hemianæsthesia.

Though the patient is able to move the anæsthetic limb voluntarily, he has no knowledge of its position or of the resistance which may be offered to its intended movement. Bastian,[45] however, maintains that "the rule has been with the hemianæsthetic patients which have been so thoroughly investigated by Charcot at the Salpêtrière that, although there has been complete loss of tactile sensibility, and usually absolute insensibility to pain in the skin and all other sensitive structures on the affected side, together with paresis of the affected limbs, the so-called 'muscular sense' has been nearly always preserved."

On this question I have appealed to M. Charcot himself. He has favoured me with a reply, from which I quote the following: "Cases of hysterical hemianæsthesia may be seen both in men and women affecting only the superficial integument, and without implication of the muscular sense, but the obnubilation, or complete disappearance of the muscular sense—in particular the loss of the sense of position of the limbs—is each very frequent, one might almost say habitual, in hysterical hemianæsthesia, especially when it is accompanied by paresis or hemiplegia....... Up to the present I have not met with serious impairment, strictly limited to the muscular sense in hysteria, unaccompanied by cutaneous hemianæsthesia. It appears from all this that the aboli-

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44 *Archiv d. Heilkunde*, 1874, Bd. xv, p. 44.
45 The Muscular Sense, *Brain*, vol. x, 1889.

tion of the muscular sense represents the highest degree of the hemianæsthetic scale." He refers me also to cases of anæsthesia[46] in which the sense of position or the limbs was entirely abolished and "yet the patients were able to move the affected members freely even when the eyes were closed. Under such conditions, however, the movements of the limbs deprived of the muscular sense are uncertain and hesitating."

These and similar facts show that the sense of movement is not essential either to the due co-ordination or power of carrying a movement into effect. Vision may entirely replace the muscular sense, though, as one would naturally expect, volitional movements effected only through the aid of vision are, when the eyes are closed, less certain and precise that those which are accompanied also by a sense of movement. Yet these defects are capable of being overcome in large measure by practice; so that, even when the eyes are closed, the visual conception of the movement is capable of compensating entirely, or almost entirely, for the loss of the muscular sense. That this does not occur in all cases may be admitted, but the essential point is that it may in some, and one case of this kind is sufficient to demonstrate that volitional action is not necessarily bound up with sensations conditioned by the muscular action itself.

It is conceivable that ideas of movements might be formed, and volitional movements effected by a brain consisting only of visual and motor centres. Under these circumstances, however, vision would be largely occupied in directing movements, and the range of muscular action and muscular adaptation would be infinitely less than if these were guided, also, by sensations generated by the movements themselves. By the so-called muscular sense, we are able to conceive and execute movements which we have never seen, but we are unable to conceive or volitionally execute movements which we have neither seen nor felt. But though, under ordinary conditions, the sensations of movement are the invariable accompaniment of muscular action, and are repeated as often as the muscular action itself, this constant association does not imply that the one is dependent on the other, or that the musculo-sensory ideas of movement are the necessary or immediate excitants of the movement itself.

Bastian holds that in addition to the conscious impressions which accompany muscular action, and which he admits may be, chiefly at least, localised in the falciform lobe, there are a set of unfelt impressions which guide the motor activity of the brain by

46 *Diseases of Nervous System* (Sydenham Society), vol. iii, pp. 304, 445, 463.

automatically bringing it into relation with the different degrees of contraction of all the muscles which may be in a state of action. To these unfelt impressions he gives the name "kinæsthesis," and he considers that the motor centres are the seat of the "kinæsthesis" or sense of movement. The so-called motor centres are, therefore, according to him, in reality sensory centres which excite the true motor centres of the spinal cord through the pyramidal tracts which connect them therewith. I cannot agree with Bastian in including in the muscular sense, which is so essentially an act of conscious discrimination, the mere afferent or unconscious impressions, through the agency of which the harmonious co-ordination of the different segments of the spinal cord and lower centres is secured, apart from the cerebral hemispheres; nor do I think that impressions, which practically do not rise into consciousness, can be ideally revived or enter into the composition of ideas or conceptions of movement. But if it were the case, as Bastian assumes, that the ideal revival of kinæsthetic impressions is the immediate excitant of the true motor centres in the spinal cord, it would follow that the so-called motor centres would be independent centres of activity, irrespective of the stimuli from the sensory centres of the cortex. Experiments show, however, that the motor centres are not independent centres of action, for it has been found by Marique,[47] whose experiments have been confirmed by Exner and Paneth,[48] that when the motor centres have been completely isolated, by section of the fibres which associate them with the sensory centres of the cortex, paralysis results of precisely the same character as that which occurs when they are actually extirpated. Marique proved that the same contractions were obtainable on electrical irritation of the respective centres after, as before, isolation, showing that they still retained their excitability and connection with the pyramidal tracts. These experiments indicate, therefore, that the motor centres of the cortex are not independent centres of action, but act only in response to the stimuli which proceed from the sensory centres by way of the associating fibres which connect them together.

If the true motor centres were situated only in the spinal cord, one would expect to find the spinal motor centres developed in correspondence with the motor capacities of the animal. In such case the spinal motor centres of man, in whom the motor capa-

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47 *Centres Psycho-moteurs du Cerveau*, 1885.

48 "Versuche über die Folgen der Durchschneidung von Associations-fasern am Hundehirn, *Archiv f. d. ges. Phys.*, Bd. xliv, 1889.

bilities are most varied and most perfect, should be developed far beyond those of other animals, but precisely the opposite holds For relatively as compared with the brain, and relatively as compared with the size of the animal, the spinal motor centres of man are less developed than those of the lower animals; and they are absolutely less than those of many animals whose capabilities are of the simplest order. The development of the spinal motor centres corresponds with that of the purely reflex synergic muscular combinations of the related metameres or body segments; while that of the cortical motor centres corresponds with the multiplicity and complexity of the motor faculties, volitional and cognitive.

From the various considerations above advanced I conclude that the motor centres of the cortex are not the centres of tactile or general sensibility, nor are they the centres of the muscular sense, whether we regard this to depend on centripetal impressions, conscious or unconscious, or on a sense of innervation; but that they are motor in precisely the same sense as other motor centres, and, though functionally and organically connected, are anatomically differentiated from the centres of sensation general, as well as special.

Frontal Centres.

The region of the brain which lies in advance of the Rolandic area and marked off by the precentral sulcus is one respecting the functions of which there is still considerable doubt. Anatomically it is related to the motor tracts of the internal capsule. These tracts, according to the investigations of Flechsig, lie in the inner portion of the foot of the crus, and connect the frontal lobe with the opposite cerebellar hemisphere indirectly through the grey matter of the pons. Destructive lesions of the frontal centres, both of the postfrontal and prefrontal regions, as I have shown experimentally, 'cause descending degeneration of these tracts[49] not capable of being followed beyond the upper part of the pons. The direction of the degeneration may be taken as a proof of the motor significancation of the regions in question. Similar degenerations have been described by Brissaud[50] as the result of lesions of the frontal lobe in man. He has not been able to trace the degeneration into the pyramid, and concludes that the internal tracts of the foot of the crus connect the frontal regions with the motor nuclei of the medulla. Degenerations in this part of the crus have, according to his observations, been always associated with

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[49] See Fig. 122, *Functions of the Brain.*

[50] *Contraction Permanente des Hemiplegiques*, 1880.

psychical defects, apart from paralysis of the face or limbs. The effects of electrical irritation, combined with those of destruction, more particularly of the postfrontal region, indicate that this part is related to the lateral movements of the head and eyes. Irritation, as we have seen, causes opening of the eyes, dilatation of the pupils, and conjugate deviation of the head and eyes to the opposite side. At the moment of destruction of this region in the one hemisphere there always occurs a temporary deviation of the head and eyes to the side of lesion. This, however, is only transient even when the destruction has been almost if not absolutely complete. In two experiments which I have described,[51] after bilateral destruction of the postfrontal area the animals were unable to turn the head or eyes to either side for a day after the operation. At first they were unable to look round when sounds were made in proximity to the ear; or, if they did, they moved the trunk and head *en masse.* The removal of the prefrontal regions alone caused no discoverable physiological symptoms, either sensory or motor. But I found in several instances that after the symptoms which followed destruction of the postfrontal area had entirely disappeared, the subsequent destruction of the prefrontal area induced paralysis of the head and eyes of exactly the same nature as before. I have confirmed these observations in a recent experiment. After apparently the most thorough cauterisation of the whole of the excitable frontal area, convex as well as mesial aspect, the animal, which at first exhibited marked distortion of the head and eyes to the side of lesion and inability to turn them to the opposite side, recovered within three days to such an extent that the defects were no longer perceptible.

A month later, extirpation of the prefrontal region, in advance of the former lesion, induced the same condition as before, namely, deivation of the head and eyes to the side of lesion, and total inability to turn them to the opposite side. The conjugate deviation of the eyes continued for some time after the movements of the head had been recovered, but within three days no defect was any longer capable of being made out in this respect. These facts indicate that the prefrontal regions have the same functional relations as the postfrontal. The transitory duration of the symptoms would be explained by the fact that the postfrontal centres were not entirely destroyed. It is difficult to remove the whole frontal area without inflicting injury on the head of the corpus striatum.

In one case in which I removed the frontal lobe on both sides

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[51] Experiments 19 and 20, *Phil. Trans.*, Part ii., 1884.

by a transverse incision immediately anterior to the precentral sulcus, the animal lived only twenty-four hours. There was no paralysis of the facial muscles or limbs, though the right limbs were used with somewhat less energy than the left. Though the animal could extend its head and trunk, it was unable to maintain an upright position, or to move its head and eyes laterally. The eyes were kept shut except when it was in any way disturbed. Sight, hearing, and tactile sensibility were unimpaired. Except the inability to move the head and eyes there was no defect observable, sensory or motor. In this case the corpora striata were also injured, more on the left side than the right.

I have recently extirpated practically the whole of the frontal region of the left hemisphere (see Fig. 35). When the animal

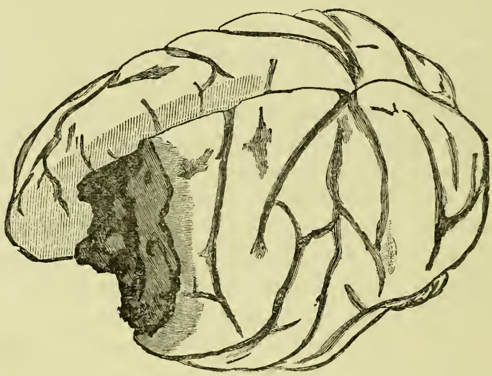

Fig. 35.

began to move about, a few hours after the operation, it was observed to turn round from right to left, and the head, when at rest, tended towards the left side. The right eyelid drooped considerably, and the right pupil was distinctly smaller than the left. Next day the conjugate deviation of the eyes continued, and they could not be turned to the right, but the lateral distortion of the head was not so pronounced. The inclination of the head towards the left gradually diminished, but the inability to turn the eyes to the right continued during the whole time of the animal's survival. It died suddenly from cerebral hæmorrhage ten days after the operation. In this case the conjugate deviation of the eyes continued longer than I had observed it in any former experiment, and this was no doubt in relation with the almost if not complete removal of the frontal lobe.

This experiment shows that destruction of the frontal region causes not only conjugate deviation of the head and eyes, but also a temporary paralysis of those movements which are also excited by electrical stimulation, namely, elevation of the eyelids and dilatation of the pupils. This confirms a similar observation which I had previously recorded. There is reason for believing, therefore, that the lateral movements of the head and eyes are not capable of being permanently paralysed, unless every portion of the frontal region be completely destroyed.

Beyond these, I have not been able to discover any other physiological symptoms on removal of the frontal lobe. I have never observed any affection of vision. Hitzig,[52] however, states that this occurs on destruction of the prefrontal region in dogs. I cannot corroborate this from my experiments on monkeys. What looks somewhat like impairment of vision towards the opposite side after unilateral extirpation of the frontal region is due to the conjugate deviation of the eyes to the opposite side, so that the animal, being unable to turn its eyes to the opposite side, does not see an object until it crosses the middle line; but the field of vision is otherwise normal. Munk finds that destruction of the frontal area in dogs causes paralysis of the trunk muscles, and he terms the frontal region the sensory sphere of the trunk, though he distinctly states that he has been unable to discover any evidence of anæsthesia. My own experiments, as well as those of Horsley and Schäfer, Hitzig, Kriworotow and Goltz, are opposed to the statements of Munk in this respect; and Horsley and Schäfer have shown that the centres for the trunk muscles are in the marginal convolution. It is probable, therefore, that any affection of the movements of the trunk which Munk may have observed has been due to direct or indirect implication of these centres. In addition to the paralysis of the movements of the head and eyes on destruction of the frontal lobes, I have also observed (and my observations have been confirmed by Hitzig and Goltz) a noteworthy psychical defect—a defect which I have endeavoured to correlate with the inability to look at, or direct the gaze towards, objects which do not spontaneously fall within the field of vision. It is a form of mental degradation which appears to me to depend on the loss of the faculty of attention, and my hypothesis is that the power of attention is intimately related to the volitional movements of the head and eyes. On this point, however, which I have elsewhere discussed, I will not on this occasion dilate further. The recorded cases of injury and disease of the frontal lobes in man are in accordance with the negative

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[52] *Archiv für Psychiatrie*, 1887, Vol. 15, p. 270.

character of experimental lesions, unilateral or bilateral, so far as relates to the sensory and motor faculties in general; and in several a certain intellectual deficiency and instability of character have been observed, not unlike those occurring in monkeys and in dogs. Of fifty-seven cases of lesion of the frontal region, collected from various sources, in two there was conjugate deviation of the head and eyes; twelve in which intelligence was specially impaired; and in all a total absence of paralysis of the limbs.

Though I have occupied so much of your time, I have only been able to treat of—and that in many respects very imperfectly—the functions of the cortical centres so far as concerns sensation and motion. There is another question which I have not considered at all, namely, the relations of the cerebral hemispheres to the functions of organic life. This, however, is a subject which is still involved in so much obscurity, and in reference to which there are at present so few facts which are not susceptible of different modes of interpretation, that I think it well to wait for further light before hazarding any definite views of my own. And I feel it all the less necessary to do so, seeing that the subject in one of its principal aspects, namely, the relation of the hemispheres to the thermic functions of the body, has been recently so ably placed before you by my predecessor, Dr. MacAlister.

On the psychical aspects of cerebral localisation I have touched only incidentally. This of itself would require a volume, and that mainly of speculation. As to the questions which I have treated more fully, and on which so many differences of opinion at present exist, and will probably still continue, I shall be content if the facts and considerations which I have brought before you contribute to their solution, if only by stimulating work on the part of others, with a view to arriving at conclusions which shall be acceptable alike to physiologists and physicians. For the true conception of the functions and relations of the cerebral hemispheres, and their constituent centres is not only of the highest scientific and philosophical interest, but of direct and important practical bearing on the diagnosis and treatment of cerebral disease.

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